OS 102

Bulletin of the British Ornithologists' Club

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MEETINGS are normally held on the ground floor of the Sherfield Building of **Imperial College**, South Kensington, London, SW7. The suite is called the **Tower Rooms** and meetings will take place in **Section A** with the entrance opposite the Queen's Tower in the main quadrangle. The nearest Tube station is at South Kensington; a map of the area will be sent on request. (Limited car parking facilities can be reserved at a special reduced charge of **£5**, on prior application to the Chairman.)

The evening will commence with a talk beginning at 6.00 pm. After the talk the cash bar will open so that attendees can socialise and at *c.*7.30 pm there will be a light buffet supper costing **£15 per person** for those who have ordered it in advance. Vegetarian and gluten-free options will be available for those who have requested them when booking.

The meetings are open to all, not just BOC members. There is no charge to attend the talk but it is necessary to register, at least a day in advance of the meeting.

FORTHCOMING MEETINGS

See also BOC website: **http://www.boc-online.org**

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29 March—Joe Tobias—*Singing in the rainforest: ornithological adventures in Amazonia*

Abstract: The forests of the Amazon basin support an incredible number of bird species, up to 600 at a single locality, and yet even the most basic details of their biology remain very poorly known. This talk describes the results of recent field work in Peru, Bolivia and Brazil, and hopes to shed a little light on some abiding mysteries, from the duet song of the antbirds to the origins of Amazonian diversity.

Biography: Joe Tobias studied the behavioural ecology of Robins *Erithacus rubecula* in Cambridge Botanical Gardens for his PhD, before working in international bird conservation for a decade. He returned to academia to study the evolutionary biology of tropical birds, and is now a lecturer based at the Edward Grey Institute for Field Ornithology in Oxford.

Those wanting to order the buffet supper should apply to the Chairman (address below) by **15 March 2011**

To comply with Imperial College requirements, those wishing to attend the talk must notify the Chairman no later than **Monday 28 March 2011**

5.40 pm 14 June—Annual General Meeting—*followed by short talks commencing at 6.00pm*
If you wish to give a talk, which should last 10–15 minutes, please send details to Robert Prŷs-Jones (e-mail: r.prys-jones@ulun.ac.uk) no later than 30 April 2011

Those wishing to order the buffet supper should apply to the Chairman (address below) by **31 May 2011**
To comply with Imperial College requirements, those wishing to attend the talks must notify the Chairman no later than **Monday 13 June 2011**

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11 October—Details will appear in the next Bulletin.

Saturday 12 November 2011—Birds of South and Central America: recent advances in knowledge. This is a joint BOC/Neotropical Bird Club/Natural History Museum meeting at the Natural History Museum, South Kensington, London. The programme is not yet finalised but the meeting is expected to begin with coffee at 10.30 and it will end at 17.00.

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BRITISH ORNITHOLOGISTS' CLUB

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CLUB ANNOUNCEMENTS

Chairman's message

Will all members who are planning to attend Club meetings please note that, contrary to what I said in my December message, in order to meet Imperial College requirements, it is necessary to register with me if you wish to attend evening meetings. You just need to e-mail or telephone me no later than the day before the event.

Subscriptions were due for renewal on 1 January 2011. If you have not already paid, please do so as soon as possible to avoid the need for further reminders.

Helen Baker

ANNUAL GENERAL MEETING

The Annual General Meeting of the British Ornithologists' Club will be held in Room SALC3, Sherfield Building, Imperial College, London SW7 2AZ, at 5.40pm on Tuesday 14 June 2011.

AGENDA

1. Minutes of the 2010 Annual General meeting (see *Bull. Brit. Orn. Cl.* 130: 73–74)
2. Chairman's report
3. Trustees Annual Report and Accounts for 2010 (both will be available before the start of the meeting)
4. The Bulletin Editor's report—Mr G. M. Kirwan
5. Publications report—Revd. T. W. Gladwin, Chairman JPC
6. Election of Officers. The Committee proposes that:
   i. Mr D. J. Fisher, currently acting Vice Chairman, be elected as *Vice Chairman*
   ii. Dr R. P. Prŷs-Jones, currently acting Hon. Secretary be elected as *Hon. Secretary*
   iii. Mr D. J. Montier be re-elected as *Hon Treasurer*
   iv. Mr R. R. Langley be elected to serve on the Committee (*vice* Mr S. A. H. Statham, who remained on Committee after resigning from the post of *Hon. Secretary* on 31 December 2010).
5. No other changes to the Committee are proposed as all other members are eligible to serve at least one more year in office.
6. Any other business, of which advance notice has been given.

The 963rd meeting of the Club was held on Tuesday 21 September 2010 in the Rector's Residence, Imperial College, South Kensington, London SW7 2AZ. Eighteen members and four guests were present.

Members attending were: Miss H. BAKER (*Chairman*), Cdr. M. B. CASEMENT, RN, Prof. R. A. CHEKE, D. J. FISHER, F. M. GAUNTLETT, Dr A. G. GOSLER (*Speaker*), D. GRIFFIN, K. HERON JONES, R. H. KETTLE, R. R. LANGLEY, D. J. MONTIER, R. C. PRICE, Dr R. P. PRŶS-JONES, R. J. PRYTHERCH, P. J. SELLAR, S. A. H. STATHAM, M. J. WALTON and P. J. WILKINSON.

Guests attending were: Mrs C. R. CASEMENT, Mrs M. H. GAUNTLETT, Mrs J. HERON JONES and Mrs M. MONTIER.

After dinner Dr Andrew Gosler gave a presentation on *Eggs dressed and undressed*. This talk brought up to date the speaker's work on eggshell pigmentation since his talk to the BOC on 7 December 2004. An important study conducted after that presentation, on the relationship between eggshell pigmentation, shell thickness and DDT contamination in the Eurasian Sparrowhawk *Accipiter nisus* had developed directly from the discussion following the earlier talk. Dr Gosler was therefore delighted to be speaking again to the Club and looked forward to yet more insightful comments.

The current talk started with a recap of the principal points presented previously. Studies of Great Tit *Parus major* eggs in Wytham Woods had shown that such pigmentation was intimately related to eggshell structure, calcium availability and water loss in incubation (Higham & Gosler 2006). The more recent work had shown that the pigment spots on Great Tit eggs marked areas of thinner shell, and that shell thickness, especially around the widest part of the egg (here referred to as the shoulder) was related to a measure of

pigment pattern known as 'spread'. This pigment spread measure appeared to have no heritable element, i.e. variation was influenced entirely by environmental factors. An important environmental factor was local calcium availability, which affected the birds through its effect on the density of small snails (Jubb *et al.* 2006), which were the chief source of calcium for females during egg formation. So, in areas where calcium was in short supply, there were fewer snails, and the tits laid thinner-shelled eggs, which showed a greater spread of pigment. Over the last 20 years this pigment spread measure had declined strikingly, which reflected a significant decline observed in soil calcium in Wytham. The most likely cause of this was thought to be acid precipitation, which had the potential to leach calcium even from soils overlying limestone.

The *Accipiter nisus* study had developed from Prof. Cheke's earlier suggestion that, if protoporphyrin pigment were incorporated within the eggshell to compensate (strengthen) for shell-thinning, because DDT was known to cause eggshell thinning in the species, perhaps it also affected shell pigmentation. The subsequent study, here reported, showed a complex relationship between pigmentation, shell thickness and DDE content of eggs, but that essentially it was correct that in this species also, protoporphyrin was incorporated where the shell was thinner, and that this occurred more in eggs that contained higher concentrations of DDE (Jagannath *et al.* 2008). That the apparent adaptation of adding this pigment where the shell was thinner had been found in such distantly related species as Great Tit and Eurasian Sparrowhawk (the latter being a species whose diet should prevent it normally from being calcium stressed) suggested that this might be a very primitive adaptation in birds.

Dr Gosler also presented some micrographs of Great Tit eggshell sections showing the layered distribution of pigments through the shell. In discussion after the talk, the suggestion that this might strengthen the shell by forming a laminate structure caused much interest.

References:

Higham, J. P. & Gosler, A. G. 2006. Speckled eggs: water-loss and incubation behaviour in the great tit *Parus major*. *Oecologia* 149: 561–570.

Jagannath, A., Shore, R. F., Walker, L. A., Ferns, P. N. & Gosler, A. G. 2008. Eggshell pigmentation indicates pesticide contamination. *J. Appl. Ecol.* 45: 133–140.

Jubb, M., Wilkin, T. A. & Gosler, A. G. 2006. Soil calcium and the local abundance, distribution and diversity of woodland snails (*Mollusca*). *Ardea* 94: 59–70.

The 964th meeting of the Club was held on Tuesday 2 November 2010 in the Sherfield Building, Imperial College, South Kensington, London SW7 2AZ. Fifteen members and four guests were present.

Members attending were: Miss H. BAKER (*Chairman*), Cdr. M. B. CASEMENT, RN, D. GRIFFIN, K. HERON JONES, M. C. JENNINGS (*Speaker*), R. H. KETTLE, R. R. LANGLEY, Dr C. F. MANN, D. J. MONTIER, R. C. PRICE, Dr R. P. PRŶS-JONES, S. A. H. STATHAM, C. W. R. STOREY, R. P. WEBSTER and P. J. WILKINSON.

Guests attending were: Mrs J. HERON JONES, Miss L. JENNINGS, P. JENNINGS and H. VON GROUW.

After dinner Mr Michael Jennings gave a presentation on the *Atlas of the Breeding Birds of Arabia (ABBA) project*, an overview on the issues which fashion bird distribution in Arabia and species conservation. The atlas started in 1984 with the objective of defining the breeding distribution and ecological requirements of birds in Arabia, i.e. the Arabian Peninsula and the Socotra archipelago (Yemen). The project reviewed published sources and some museum specimens, but the main source of distributional data was from nearly 500 field observers; his own surveys (40 between 1985 and 2009) were to those corners of Arabia poorly studied by others. Bird distribution in Arabia is a result of a number of important factors. Over large areas the arid climate restricts breeding species to a few Saharo-Indian arid-land specialists, often with a nomadic tendency. The topography and habitats of Arabia include a wide range of geology; granite, sandstone, lava flows, limestone, not to mention sand dunes. Mountains rise to 3,700 m in the south-west, with *Juniperus* forests, and there are extensive mangrove swamps on the coast. The varied zoogeographical influences play a significant role. There are many Afrotropical species in the south-west (both residents and breeding summer visitors) and an Indian flavour to the eastern part of the peninsula. However, the predominant influence throughout is Palearctic. Arabia is also a centre of endemism with 11 endemic landbirds, mostly in the south-west highlands, three endemics to the seas around Arabia and nine endemics on Socotra. A stealthy change to the Arabian avifauna in recent years has been the establishment of at least 20 ferally breeding exotic birds. Major changes to the Arabian environment since about the 1970s have added many species to the avifauna, for example through the development of huge areas of irrigated agriculture and dairy farms and artificial wetlands. For example, in the well-studied area within 100 km of Riyadh, diversity has increased from 44 breeding species identified in 1977 to 88 breeding species by 2002. On the other hand, the birds of Arabia also have to contend with a wide variety of conservation pressures, overgrazing, charcoal burning, pollution, hunting and introduction of exotic predators, as well as habitat change on a grand scale. Several species are now under threat. When the atlas was published in July 2010 it included 273 confirmed breeding species and another 24 which probably breed.

REVIEW

Wells, D. R. (ed.) 2010. Systematic Notes on Asian Birds 2010. *Brit. Orn. Cl. Occ. Publ.* 5. 148 pp. UK (second class) £18; Europe air and worldwide surface £20; worldwide air £22, available from BOC Office (see inside front cover).

Between 2000 and 2006 the National Museum of Natural History (NMNH, Leiden) published, in conjunction with The Trust for Oriental Ornithology (TOO), six volumes of collected papers on the taxonomy and nomenclature of birds under the general title *Systematic Notes on Asian Birds (SNAB)*. Changes in publication policy by the NMNH interrupted this series, but now the BOC has co-operated with TOO and taken on publication. The region covered is a 'broadly defined Oriental Realm', bounded to the north-west by the farther borders of Pakistan, Afghanistan, China and Mongolia, all of which are included, and to the south-east by the edge of the Australasian Sahul shelf.

This seventh volume contains nine papers, numbered sequentially (68–76) with previous volumes, plus a letter commenting on a previous paper in the series. The first four papers consider the babblers (Timaliidae), and include an overview of the entire group based on recent molecular findings, a review of the subfamily Pellorneinae as historically recognised, with a detailed enumeration of the nomenclature of this subfamily and the existence and whereabouts of all relevant type specimens; by contrast, the fourth is more narrowly focused on problems surrounding the status of *Macronus gularis connectens* and their potential resolution. Two further papers, both by Jiří Mlíkovský, provide equivalent broad taxonomic reviews and type specimen enumerations for Asian grebes (Podicipedidae).

The remaining papers are more diverse. Two consider the validity of *Sitta villosa corea* and contentious aspects of the ornithology of Bangka Island, Indonesia, respectively. In much the longest paper in the volume, Jochen Martens reviews the complex leaf warbler genera *Phylloscopus* and *Seicercus*, which have been the subject of much recent taxonomical research. A total of 50 *Phylloscopus* species are recognised, an increase of 50% in the 25 years since the relevant volume of Peter's *Checklist of birds of the world*. *Seicercus* is clearly not monophyletic, its species all forming part of the *Phylloscopus* molecular phylogenetic tree. However, the nine species recognised are for now retained in *Seicercus*, pending finalisation of a comprehensive molecular taxonomy of all taxa within the two genera. This paper brings together a large amount of information in a convenient, comparative form.

Systematic reassessment of the Asian avifauna has tended to lag behind that of other analogous geographical areas. The continuing series of papers encompassed by *SNAB* has established itself as an important source of information on Oriental avian taxonomy, nomenclature and distribution, and should be referenced by all interested in these topics.

Robert Prŷs-Jones

Unravelling the ecological radiation of the capuchinos: systematics of Dark-throated Seedeater *Sporophila ruficollis* and description of a new dark-collared form

by Juan Ignacio Areta, Jorge Ignacio Noriega, Luis Pagano & Ignacio Roesler

Received 8 March 2010

Summary.—The diverse genus *Sporophila* has a complex systematic history. A new dark-collared form of *Sporophila* seedeater, herein described on the basis of three adult males, resembles male *S. ruficollis* but has a dark nape and rufous back. We informally name the new form 'caraguata' for its preferred habitat. We tested four hypotheses regarding the systematic situation of the 'caraguata' form: valid species, hybrid *S. ruficollis* × *S. cinnamomea*, colour morph of *S. cinnamomea*, and colour morph of *S. ruficollis*. Vocally and ecologically, the 'caraguata' form cannot be diagnosed from *S. ruficollis*. This evidence strongly suggests that *S. 'caragnata'* is a colour morph of *S. ruficollis*, although a hybrid origin is hard to assess and cannot be discarded. *Sporophila ruficollis* differs in preferred habitat, plumage and vocalisations from the rest of the capuchinos, and must be considered a valid species. The pattern of morphological variation exhibited by dark-throated and grey-backed *S. ruficollis* and dark-collared and rufous-backed 'caraguata' is repeated in the white-throated and grey-backed Marsh Seedeater *S. palustris* and white-collared and rufous-backed Entre Ríos Seedeater *S. zelichi*; moreover, the members of each pair are indistinguishable ecologically and vocally. The 'fuzzy' species borders and complicated taxonomy of the *ruficollis* group could stem from an ongoing evolutionary radiation in the capuchinos. This radiation has apparently proceeded with little genetic divergence, simple changes in colour of male plumage, virtually no differences in females, and little morphological change in size and shape, but marked divergence in habitat use and voices of the involved forms.

Sporophila is a large and diverse genus of *c.*30 species, almost confined to the Neotropics (Ouellet 1992). Because of their short strong bills, they were historically placed with the true finches (Emberizini). However, recent morphological and molecular studies have revealed that they are allied to tanagers (Thraupini) in the tanager-finches group, and their short strong bills are a convergence attained for eating seeds (Clark 1986, Sibley & Ahlquist 1990, Klicka *et al.* 2000, Lijtmaer *et al.* 2004).

Classification of the genus *Sporophila* has been difficult at all levels, from family placement of the genus to colour morph status of several forms. Most revisions and systematic evaluations have relied heavily on plumage characters, making little use of natural history data (Sclater 1871, Hellmayr 1938, Meyer de Schauensee 1952, Olson 1981, Restall 2002, Stiles 2004). Studies of systematics have also largely ignored vocalisations, although these are among the most useful characters for resolving such riddles (Schwartz 1975, Areta 2008).

Systematics have been particularly confusing for the Phyrrhomelanae, a group originally defined by Bonaparte (1850) to include all of the essentially rufous and black / grey *Sporophilae*, which includes among other taxa those we now recognize as capuchinos:

the 'coloured-cheeked capuchinos' Dark-throated Seedeater *S. ruficollis*, Rufous-rumped Seedeater *S. hypochroma*, Chestnut Seedeater *S. cinnamomea*, Marsh Seedeater *S. palustris*, Entre Ríos Seedeater *S. zelichi*, Tawny-bellied Seedeater *S. hypoxantha*, Black-and-tawny Seedeater *S. nigrorufa*, Capped Seedeater *S. bonvrcnil*, and the 'grey-cheeked capuchinos' Ruddy-breasted Seedeater *S. minuta*, Chestnut-bellied Seedeater *S. castaneiventris* and Black-bellied Seedeater *S. melanogaster* (Sick 1997, Lijtmaer *et al.* 2004). Despite the paucity of data, a number of different systematic treatments have been proposed for the *ruficollis* group, i.e. *S. ruficollis* to *S. hypoxantha* as defined above (Sclater 1871, Hellmayr 1904, 1938, Meyer de Schauensee 1952, 1966, 1970, Short 1969, 1975, Paynter & Storer 1970, Narosky & Yzurieta 1987, de la Peña 1989, Ridgely & Tudor 1989, Ouellet 1992, Pearman & Abadie 1995, Silva 1999, Areta 2008, Remsen *et al.* 2009). For example, *S. hypochroma* has been treated as a species (Short 1969, Paynter & Storer 1970), suggested to be a morph of *S. cinnamomea* (Ridgely & Tudor 1989) or treated as conspecific with *S. castaneiventris* (Meyer de Schauensee 1952). Likewise, *S. palustris* is usually treated as a valid species (Hellmayr 1938, Remsen *et al.* 2009), but it was suggested to be a colour morph of *S. hypoxantha* (Short 1975) and *S. zelichi* was recently shown to be a morph of *S. palustris* or a hybrid (Areta 2008). Moreover, females of most (but not all) capuchinos are essentially indistinguishable (Hellmayr 1938) and genetic analyses have failed to clarify the relationships of the different forms because of very shallow and inconsistent differences, especially in the *ruficollis* group (Lijtmaer *et al.* 2004, Kerr *et al.* 2009).

During field work in Entre Ríos province, Argentina, aimed to elucidate the systematics of capuchinos, JIA met many bird-keepers who mentioned a form 'identical to *S. zelichi* but with a black instead of white collar' (Figs. 1–2). Dr M. Zelich, the collector of the type specimens of *S. zelichi*, had been aware of this dark-collared form since at least 1969 and had collected two males (M. Zelich pers. comm.; Graham-Yool 2003). These specimens were loaned to S. Narosky, together with the types of the soon to be described *S. zelichi* (Narosky 1977). Despite this, Narosky (1977) did not mention the dark-collared specimens. The whereabouts of these specimens are uncertain, since they were either reported lost by S. Narosky prior to his description of *S. zelichi* (M. Zelich pers. comm.), or returned to Dr M. Zelich (S. Naroksy pers. comm.). The illustration as well as the description erroneously assigned to *S. ruficollis* by Armani (1985) agree well with this overlooked diagnostic plumage; thus, the first published reference to the dark-collared form has not been recognised until now. Pearman & Abadie's (1995) comment that an 'as yet undescribed, *Sporophila* form has been observed twice in south-east Entre Ríos province' also refers to this form (M. Pearman *in litt.* 2007). We observed a presumed subadult male of this form in Corrientes province in Argentina and continued our quest among bird-keepers until, in January and March 2006, we found some that had trapped the bird in the wild. Because unnamed objects are more difficult to reference, we propose the informal name 'caraguata' for this dark-collared form for its preferred habitat of stands of *Eryngium horridum* (Apiaceae) known locally as 'caraguatá'. We use quotation marks to denote that this is neither a subspecies nor a species but at the same time recognise it as a morphologically diagnosable form of seedeater.

The unexpected existence of this diagnostic seedeater opens a door to understanding the radiation of Neotropical seedeaters. Here we (1) describe the new 'caraguata' form of *Sporophila ruficollis*, (2) evaluate four hypotheses regarding its taxonomic status based mainly on comparisons of vocalisations and habitat use with *S. ruficollis* and *S. cinnamomea*, (3) discuss the systematics of *S. ruficollis*, and (4) set the discoveries in perspective within the capuchinos clade by discussing the apparently radiating nature of diversification in the capuchinos and the systematic challenges that arise from these.

Methods

We searched for capuchinos during four breeding seasons between October 2003 and March 2007. Sampling effort totaled 70 days at 26 locations: one day at one location in Buenos Aires (Argentina), 33 days at 11 locations in Entre Ríos (Argentina), 28 days at seven locations in Corrientes (Argentina), three days at two locations in Santa Fé (Argentina), three days at two locations in Paysandú (Uruguay) and three days at three locations in Rocha (Uruguay) (Fig. 3).

We recorded vocalisations using a directional microphone (Sennheiser ME-67) with a Rycote 6 Kit (shock-mount, windshield and windjammer) and a tape-recorder (Marantz PMD-222). Spectrograms were prepared using Syrinx 2.1 (J. Burt, www.syrinxpc.com). Additional recordings were provided by other observers (see Appendix 1). All recordings by JIA are archived at the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, NY).

The songs of capuchinos include many different, non-repetitive and morphologically complex notes. To compare vocalisations, we first characterised notes which, based on shape (including duration and frequency distribution) and relative position in the songs, could be identified unambiguously despite variation among individuals. We then compared the frequency of occurrence of these notes in individuals within and among forms.

To characterise habitat use, we assigned each territorial bird to one of four broad habitat categories: (1) caraguatal-cardal, (2) undulating grassland, (3) depressed Pampas grasslands, and (4) annual crops. Caraguatal-cardal is dry grassland on generally level ground with large stands of *Eryngium horridum*, locally known as 'caraguatá' and naturalised thistles (*Carduus* spp.), isolated *Bacharis* spp. shrubs, and occasional *Acacia caven* and *Prosopis affinis* trees. Undulating grassland included upland grasslands on the ridges, valleys and slopes of the Mesopotamian grasslands of Entre Ríos and Corrientes, and close to the Uruguay River in Paysandú. Typical features include rocky outcrops, sandy soils, diverse grasses (e.g., *Paspalum*, *Bromus*, *Piptochaetium*), and occasionally Yatay palms (*Butia yatay*). Depressed Pampas grasslands comprised *Paspalum quadrifarium* and *Spartina densiflora* grassland with occasional *Eryngium* sp. growing on salty soils, in Buenos Aires province. Annual crop habitats were large-scale annual crops, including 'soy' *Glycine max*, 'rice' *Oryza sativa* and 'corn' *Zea mays*, and were present throughout. These habitats are widespread at the geographical scale, and they might co-exist in a mosaic at a single locality or in a reduced geographic area (i.e., the habitats might inter-digitate at the same locality). Although our broad habitat categories may mask subtle habitat segregation at a finer scale, they were designed to apply over a wide area where more detailed descriptions would have precluded the discovery of any habitat-use pattern because many features unique to each site would have masked overall similarities (see sampling localities in Appendix 2).

Because individuals were not marked, we included only data from territorial males that were spatially or temporally segregated to avoid pseudo-replication. For areas visited more than once, we included only one record per territory. We considered each contact to be an independent sample appropriate to evaluate habitat preference, by comparing frequency of occurrence of each form in each habitat. Preferred habitat was defined as that where we found at least 65% of territorial males. Habitat overlap was calculated as the proportion of encounters where two or more species shared a habitat.

We studied plumages and measured bill length (exposed culmen), wing chord, tail length and tarsus length of 67 *S. ruficollis*, nine *S. cinnamomea* and one 'caraguata' from specimens held at the American Museum of Natural History (AMNH, New York), Fundación Miguel Lillo (FML, Tucumán, Argentina), Museo Antonio Serrano (MAS,

Paraná, Entre Ríos, Argentina), Museo Ornitológico de Berisso (Berisso, Buenos Aires, Argentina), Museo de La Plata (MLP, La Plata, Argentina) and Museo Nacional de Historia Natural (MNHN, Montevideo, Uruguay) (Appendix 3). A second 'caraguata' was measured as a live specimen held at CICyTTP-CONICET, Diamante, Argentina. Means for all measurements were compared statistically using two-tailed student's t-test (alpha=0.05).

Systematic hypotheses.—Following Areta (2008), we considered four hypotheses regarding the possible specific validity, hybrid origin, or morph condition of the 'caraguata' form (Table 1). These hypotheses stem from the nature of its plumage, apparently intermediate between that of *S. cinnamomea* and *S. ruficollis* (see below), and so here we focus our hypothetical framework on comparisons between these forms, although they can easily be extrapolated to any other set of forms in the group (see Areta 2008, 2010). To avoid subjective preference for any systematic hypothesis, we used the method of multiple working hypotheses (Chamberlin 1965). We deduced predictions for each hypothesis based on the Recognition Species Concept (Paterson 1985), whereby any bird species must have a preferred or normal habitat and a Specific Mate Recognition System (SMRS) that ensures successful reproductive encounters between members of a species (Paterson 1980, 1985, Vrba 1995). Habitat-dependent selection acting on SMRS is thus the main force thought to influence speciation, and two closely related valid species should not share the same preferred habitat. We consider vocalisations to be a key element in species-specific recognition (i.e., a crucial part of SMRS). See Slabekoorn & Smith (2002) for a review of habitat-dependent divergence in vocalisations and speciation. We used the Recognition Species Concept (Paterson 1985) to evaluate the specific status of capuchinos because this concept clearly delimits species and narrows the meaning of species to a restricted biological phenomenon, permits testing of predictions, and makes the results of our study easily interpretable by researchers endorsing other species concepts. Although many of the >30 *Sporophila* species co-exist in the same habitats, they do not regularly appear to be each other's closest relatives. However, those species we studied are one another's closest relatives and do not differ obviously in bill morphology. Differences among these capuchinos occur in male plumage, songs and preferred habitat (Areta 2008, 2010; unpubl. data). Therefore, although voice alone might serve to assess specific status of populations, a strong test of specific identity should test voice and distinctive habitat as key features of any valid species. The four hypotheses that we tested were as follows.

(1) Good species hypothesis (GSH). According to this hypothesis, the 'caraguata' form is a valid species based on its diagnostic plumage pattern. If so, we predicted that individuals would have vocalisations and a preferred habitat that differed from those of other closely related species.

TABLE 1

Four alternative hypotheses and predictions that permit for an evaluation of the systematic status of the 'caraguata' form. For each prediction, support is indicated by (+), rejection by (-) and inconclusive evidence by (±).

Hypothesis	Predictions regarding 'caraguata'	
	Vocalisations	Preferred habitat
(1) Good species hypothesis	Unique (-)	Unique (-)
(2) Hybridisation hypothesis	Intermediate between *S. ruficollis* and *S. cinnamomea* (-) or identical to *S. ruficollis* or *S. cinnamomea* (±)	Shared by both *S. ruficollis* and *S. cinnamomea* (±, -)
(3) Colour morph hypothesis I	As *S. cinnamomea* (-)	As *S. cinnamomea* (-)
(4) Colour morph hypothesis II	As *S. ruficollis* (+)	As *S. ruficollis* (+)

(2) Hybridisation hypothesis (HH). This hypothesis considers the 'caraguata' form to be a hybrid between *S. ruficollis* and *S. cinnamomea*, based on the assumption that the rufous back and dark collar of 'caraguata' might originate through hybridisation between the chestnut-bodied *S. cinnamomea* and dark-throated *S. ruficollis*. If true, we predicted that the songs of 'caraguata' would either be intermediate between *S. ruficollis* and *S. cinnamomea* (if songs are genetically determined) or identical to the paternal form (*S. ruficollis* or *S. cinnamomea*, if songs are learned). This hypothesis predicts that the habitat of 'caraguata' would be shared by both parental forms (*S. ruficollis* and *S. cinnamomea*).

(3) Colour morph hypothesis I (CMH I). This hypothesis considers the 'caraguata' form to be a colour morph of *S. cinnamomea*, because the two forms have the back and belly concolorous (both are chestnut in *cinnamomea* but rufous in 'caraguata'). If true, we predicted that 'caraguata' would have songs and preferred habitats like those of *S. cinnamomea*.

(4) Colour morph hypothesis II (CMH II). This hypothesis considers the 'caraguata' form to be a colour morph of *S. ruficollis*, since both have a dark throat and rufous belly. If true, 'caraguata' should have songs and preferred habitats like those of *S. ruficollis*.

Female capuchinos in the *ruficollis* group are indistinguishable by plumage to human observers and their vocal repertoire is usually limited to calls and soft chatters (pers. obs.). Thus, we used male songs and habitat to test all hypotheses. Distribution patterns and relative abundance were also used to assess their validity. Plumage was marginally used to test hypotheses, because plumages constitute the starting point to propose the different hypotheses and similar patterns of variation occur within and between species in the group (Areta 2010), reducing their usefulness to assess species limits in capuchinos.

Results

Description of the 'caraguata' form. *Males.*—Identical to male *S. zelichi* but black replaces the white throat and nuchal collar (Fig. 1). It is also very similar to *S. ruficollis* but the black nape and rufous back replace the grey nape and back of *S. ruficollis* (Fig. 2). Thus, in 'caraguata' the cap is grey, the throat and nuchal collar black, the rump, back and ventral patches rufous-chestnut and the wings and tail black. The black remiges show the typical white speculum of all capuchinos (Figs. 1–2).

The following descriptions are based on three males. Individual 1 is deposited at the Museo de La Plata (MLP-14044) and individuals 2 and 3 remain alive at the CICyTTP-CONICET for ongoing studies of moult sequence and plumage maturation.

Individual 1 (MLP-14044): forehead and crown lead grey. Nape and hindneck black, joining black of lores, ear-coverts, chin, throat, neck, and breast to the midline. Rufous-chestnut back, rump and abdomen from mid breast to belly and undertail-coverts. Greyish uppertail-coverts with buffy fringes. Blackish primaries with paler and silky underside. White speculum visible on folded wing and extends over base and centre of all remiges, but not on two outermost primaries and two innermost tertials. Buff fringes to greater wing-coverts and secondaries. Blackish upperwing-coverts fringed buff. White underwing-coverts with some chestnut feathers intermixed. Rectrices dorsally blackish, somewhat paler and silky on underside with buff-coloured tips visible above and below. Bill almost entirely black with a notably paler base to mandible. Iris dark brown. Grey tarsus. Captured in the vicinity of Ibicuy (Estación Holt), dpto. Islas del Ibicuy, Entre Ríos, Argentina (59°09'W, 33°44'S; Fig. 3).

Individual 2 (CICyTTP-CONICET): forehead and crown like individual 1, but with some dark rufous-chestnut feathers in crown. The nape marks ill-defined transition between grey crown and a narrow black collar extending and joining black lores, ear-coverts, chin, throat, neck and upper breast. Dark rufous-chestnut back, rump and abdomen from upper breast

Figure 1. Two *Sporophila* males of the dark-collared 'caraguata' form, perching in a caraguatá *Eryingium horridum* plant (Aldo Chiappe)

Figure 2. Comparison between the dark-collared 'caraguata' form and Dark-throated Seedeater *Sporophila ruficollis*. (A) Adult male 'caraguata' from Perdices, Entre Ríos Argentina (J. La Grotteria). (B) Adult male 'caraguata' from Las Piedras, Entre Ríos, Argentina (individual 2, see description) (J. I. Areta). (C) Adult male *S. ruficollis* from Mercedes, Corrientes, Argentina (C. Figuerero). Note the distinct black collar and rufous back of 'caraguata' vs. the black throat and grey nape and back of *S. ruficollis*.

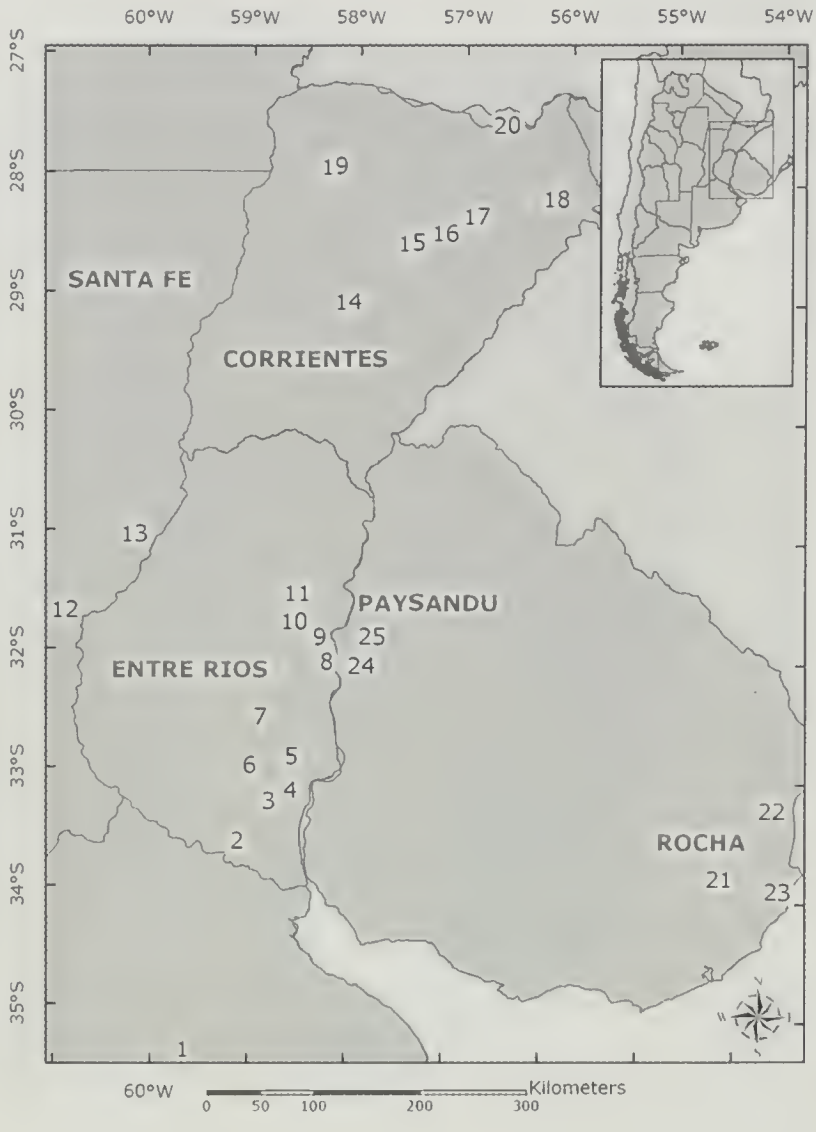

Figure 3. Location of sites visited during this study. Argentina. Buenos Aires province: 1. Saladillo (35°30′S, 59°56′W). Entre Ríos province: 2. Ibicuy (33°44′S, 59°09′W), 3. Arroyo Ñancay (33°23′S, 58°44′W) / Perdices (33°18′S, 58°42′W), 4. Estancia La Marita (33°20′S, 58°35′W), 5. Gualeguaychú (33°00′S, 58°30′W) / Las Piedras (32°53′S, 58°33′W), 6. Larroque (33°02′S, 59°00′W), 7. Urdinarrain (32°41′S, 58°53′W), 8. Puerto Liebig and Arroyo Caraballo (32°09′S, 58°11′W), 9. Parque Nacional El Palmar (31°55′S, 58°18′W), 10. Arroyo Baru (31°52′S, 58°27′W), 11. San Salvador (31°37′S, 58°30′W,). Santa Fé province: 12. Sauce Viejo (31°46′S, 60°50′W), 13. Campo del Medio (31°08′S, 60°08′W). Corrientes province: 14. Mercedes (29°10′S, 58°05′W), 15. Estancia Rincón del Socorro (28°32′S, 57°10′W), 16. Colonia Pellegrini (28°35′S, 57°10′W), 17. Cambá Trapo (28°27′S, 56°51′W), 18. Cuenca del río Aguapey (28°36′S, 56°56′W), 19. Estancia San Juan Poriahú (27°42′S, 57°11′W) / Parque Nacional Mburucuyá (28°00′S, 58°05′W), 20. Rincón Santa María (27°30′S, 56°35′W). Uruguay. Rocha Department: 21. Bañados de la India Muerta (33°45′S, 53°50′W), 22. Cebollatí (33°15′S, 53°38′W), 23. Laguna Negra (34°00′S, 53°40′W). Paysandú Department: 24. Lorenzo Geyres, Quebracho (32°04′S, 57°55′W), 25. Queguayar (32°00′S, 57°50′W).

to belly and undertail-coverts; some feathers tinged blackish close to nape impart a blurry streaking. Uppertail-coverts, primaries, speculum, greater wing-coverts and secondaries like individual 1. Upper- and underwing-coverts like individual 1, but without chestnut. Rectrices like individual 1, but with paler buff-coloured tips. Bill like individual 1, but with some horn-coloured markings, including base to mandible. Iris and tarsus like individual 1

TABLE 2

Bill length, wing chord, tail length and tarsus length of Dark-throated Seedeater *Sporophila ruficollis*, Chestnut Seedeater *Sporophila cinnamomea* and the 'caraguata' form based on specimens listed in Appendix 3. Values (in mm) as mean ± SD (*n* = sample size) [range] for *S. cinnamomea* and *S. ruficollis*. Individual measurements are given for two 'caraguata'.

	Bill length	Wing chord	Tail length	Tarsus length
S. ruficollis	8.15±0.11 (56) [7.65–8.75]	53.17±1.19 (67) [50–55]	38.37±1.78 (58) [35.0–41.5]	14.03±0.65 (64) [12.5–15.0]
S. cinnamomea	8.42±0.44 (9) [7.50–9.05]	52.82±1.37 (9) [50.95–54.45]	37.25±0.87 (4) (36–38)	13.65±0.73 (9) (12.60–14.35)
'caraguata' (1)	8.26	52.5	36.5	14.75
'caraguata' (2)	8.68	53.0	38.5	14.41

(Fig. 2). Captured 13 km north-west of Gualeguaychú at Las Piedras, dpto. Gualeguaychú, Entre Ríos, Argentina (58°33'W, 32°53'S; Fig. 3).

Individual 3 (CICyTTP-CONICET): very similar to individual 1, but differs in broader dark nuchal collar and paler ventral coloration. Captured on the outskirts of Gualeguaychú, dpto. Gualeguaychú, Entre Ríos, Argentina (58°30'W, 33°00'S; Fig. 3).

Individuals 1 and 3 differ from individual 2 mostly in being paler rufous-chestnut, lacking chestnut feathers in the crown, having a broader and better-defined black collar, a neat back without blurry streaking and a black throat extending to the mid breast.

Measurements of 'caraguata' males are indistinguishable from those of *S. ruficollis* and *S. cinnamomea* (Table 2). Two-tailed t-tests showed that bill length was marginally different between *S. ruficollis* and *S. cinnamomea* ($t(63)=2.08$, $p=0.04$) while wing-chord ($t(74)=1.99$, $p=0.42$), tail length ($t(60)=2$, $p=0.22$) and tarsus length ($t(70)=1.67$, $p=0.11$) did not differ significantly (Table 2).

Subadult male.—A presumed young male was found on 22 November 2002 at Estancia San Juan Poriahú, dpto. San Miguel, Corrientes, Argentina (57°11'W, 27°42'S, Fig. 3). Its plumage matched that expected of a young male moulting to adult plumage or a male entering or coming out of 'eclipse' plumage: plain grey crown, black lores, ear-coverts, chin, throat, breast and neck. Back, rump and abdomen pale buffy-brown, similar to females, but with a small patch of chestnut-rufous on the body-sides. Dark wings and tail fringed grey and brown as in adults. The bird did not vocalise. A bird in identical plumage was photographed by J. Spinuzza at Arroyo Ayú-í, Corrientes, Argentina, in December 2006, and birds presumably similar to this were observed with *S. ruficollis* at Iberá Marshes, Corrientes, during spring and summer 2007 / 08 by A. Ocampo (Chebez 2009).

All the above records from Corrientes are tentatively attributed to the 'caraguata' form: since no adults were recorded from these areas, we consider these identifications provisional pending further study.

A male illustrated and described in Armani (1985) as *S. ruficollis* has a complete black collar, rufous rump and belly, and a browner back, suggesting that it was moulting into its breeding, or first adult plumage, or abandoning 'eclipse' plumage. We contest Armani's identification, since his bird is clearly a male 'caraguata' and not *S. ruficollis*.

Females.—Although apparently never collected or trapped (R. Tato pers. comm.), female plumages are doubtless indistinguishable in the field from those of other females of the *ruficollis* group.

Distribution and abundance.—The 'caraguata' form is certainly known from six localities in Entre Ríos and possibly from three localities in Corrientes, all in Argentina (Fig. 3). Adult males from Entre Ríos were trapped at Las Piedras (dpto. Gualeguaychú), on the outskirts of Gualeguaychú (dpto. Gualeguaychú), at Puerto Liebig (dpto. Colón) and Ibicuy (dpto. Islas del Ibicuy). There is also a photographic record from Perdices (dpto. Gualeguaychú) (Fig. 2), and a reliable sighting from Arroyo Ñancay (dpto. Islas del Ibicuy) (D. Blanco *in litt.* 2006). The 'caraguata' male illustrated by Armani (1985) is of unknown provenance. Observations of possible subadult males from Corrientes come from Estancia San Juan Poriahú (dpto. San Miguel), Arroyo Ayú-í (dpto. Mercedes) and Iberá marshes (dpto. Mercedes). The 'caraguata' form possibly also occurs in Uruguay (J. C. Mazulla *in litt.* 2006).

Sporophila ruficollis is widespread. It breeds, in suitable habitat, in northern lowland Argentina, Paraguay, lowland Bolivia, western Uruguay and southern Brazil (Sick 1997, Mazar Barnett & Pearman 2001, Azpiroz 2003, Hennessey *et al.* 2003, Guyrá Paraguay 2004; pers. obs.). *Sporophila cinnamomea* has a restricted breeding range, in eastern Argentina, southern Brazil, and eastern and western Uruguay (Sick 1997, Mazar Barnett & Pearman 2001, Azpiroz 2003). Both *S. ruficollis* and *S. cinnamomea* are long-distance migrants and

stem-gleaning specialists (Silva 1999; pers. obs.). At least some *S. ruficollis* and *S. cinnamomea* migrate to the Cerrado of Brazil (Silva 1999, pers. obs.). The 'caraguata' form is migratory, with records spanning November–February in eastern Argentina. Its non-breeding grounds are unknown, but it probably winters together with *S. ruficollis* (see Discussion).

The 'caraguata' form exists in very small numbers in nature: while we only encountered a single male in subadult plumage in the field, a similar search effort produced >200 *S. ruficollis* males and >80 *S. cinnamomea* males.

Habitat.—Dr M. Zelich and ten bird-keepers from Entre Ríos reported capturing at least 15 individuals of this form. In all instances for which precise information is available, territorial males of the 'caraguata' form were caught in habitat typical of *S. ruficollis*: caraguatal-cardal dry grassland (*n*=12, 100%). The adult male from Perdices was in dry grassland with bushes in an agricultural area where several *S. ruficollis* had been present some days before. The sighting from Arroyo Ñancay involved a mixed-species flock of 'caraguata', *S. ruficollis* and Double-collared Seedeater *S. caerulescens* in grassland of *Panicum* cf. *bergii* (D. Blanco *in litt.* 2006). The subadult 'caraguata' from San Juan Poriahú was feeding in flooded grassland along with *S. bouvreuil pileata*, but only 50 m from a large area of caraguatal-cardal, where only *S. ruficollis* was present and abundant. Based on its passive behaviour and lack of vocalisations this subadult-plumaged bird was apparently not holding territory, but merely feeding gregariously like most capuchinos (see Discussion). We found 110 territorial males of *S. ruficollis*: 82 (74.5%) in caraguatal-cardal, just eight (7.3%) in undulating grasslands, 12 (10.9%) in depressed Pampas grasslands at the southernmost site and eight (7.3%) in annual crops. We found 34 territorial males of *S. cinnamomea*: 25 (73.5%) in undulating grassland, five (14.7%) in marsh or wet grassland and four (11.7%) in cardal-caraguatal.

In synthesis, preferred habitat of 'caraguata' and *S. ruficollis* is caraguatal-cardal, whilst *S. cinnamomea* prefers undulating grassland. All forms occur, in varying numbers, in cardal-caraguatal but in our limited sample 'caraguata' did not occupy undulating grassland like *S. cinnamomea* and *S. ruficollis*.

Vocalisations.—We sound-recorded three 'caraguata' males, 82 *S. ruficollis* males and 24 *S. cinnamomea* males (Appendix 1). Typologically, the capuchinos featured in this study have three main voice types: an introduction, a main song and various calls.

We detected geographic variation in the voice of *S. ruficollis*. This variation can be accommodated in two regiolects ('song variants encompassing extensive subpopulations of a species and all individuals within this large range', Martens 1996: 221): the Mesopotamia regiolect in Argentina and Uruguay, and the Alto Madidi regiolect in Bolivia (Figs. 4–5, Appendix 1; Areta 2010).

In the Mesopotamia regiolect, we identified an introduction and 19 notes in the repertoire of *S. ruficollis* (Fig. 4, Table 3). The introduction of *S. ruficollis* in the Mesopotamia regiolect comprises a variable number of notes (usually 2–4). Typically, the first two notes are flat, with the second slightly higher pitched than the first. If present, the third note is either flat or descending, and a fourth distinctively descending and higher pitched note can be given (Fig. 4A–B). Variation in the number of introductory notes occurs both inter- and intra-individually. The introduction can be given alone several times or as an introduction to the main song.

The typical main song in the Mesopotamia regiolect is a long complex series of variously shaped notes delivered at a leisurely pace (Fig. 4C–E). Depending on the level of excitement, singing males can vary the number of final notes in a series, sometimes even linking complete songs. Although the typical sequence of notes is depicted in Fig. 4, the sequence can be altered to follow no obvious pattern (i.e., apparently random). Such

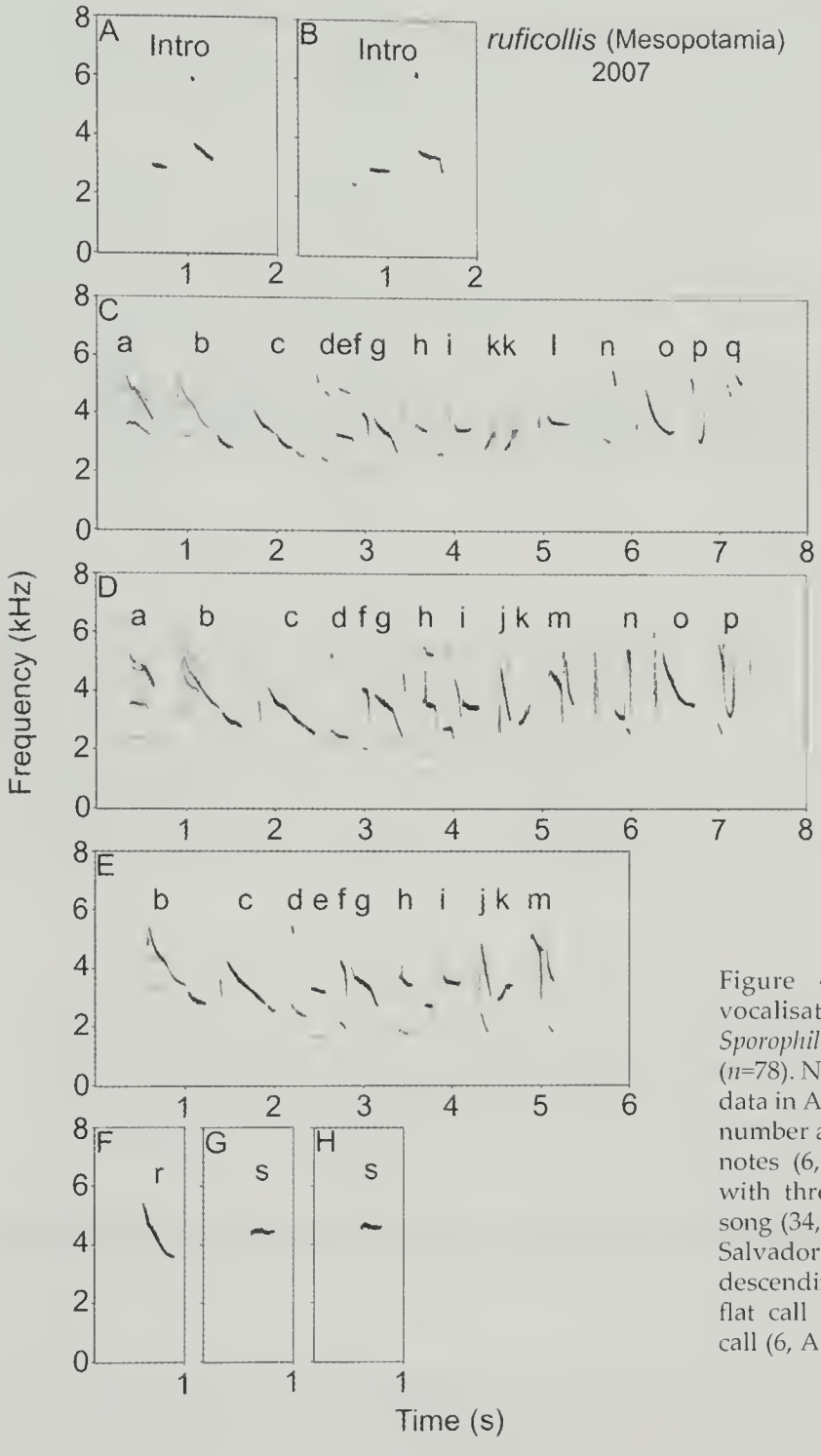

Figure 4. Representative sonograms of vocalisations of Dark-throated Seedeater *Sporophila ruficollis*, Mesopotamia regiolect (*n*=78). Numbers in parentheses correspond to data in Appendix 1, locality name and locality number as in Fig 2. (A) introduction with two notes (6, Arroyo Baru–10), (B) introduction with three notes (34, Gualeguaychú–5), (C) song (34, Gualeguaychú–5), (D) song (11, San Salvador-11), E) song (6, Arroyo Baru–10), (F) descending call (34, Gualeguaychú–5), (G) flat call (34, Gualeguaychú–5), and (H) flat call (6, Arroyo Baru–10).

variation can occur in successive songs of the same individual. Singing males can also deliver parts of the main song randomly and occasionally perform a song comprising series' of notes lacking any clear pattern. We identified two main calls in the repertoire of *S. ruficollis*: a descending arched call (Fig. 4F) and a flat high-pitched call (Fig. 4G–H).

The Alto Madidi regiolect is based on few data but we identified an introduction and 11 notes in an isolated population of *S. ruficollis* from the Apolo-Madidi savannas, Bolivia. This population shows consistent vocal differences from populations in the lowlands of Argentina and Uruguay (Fig. 5, Table 3).

We did not detect any geographical variation in voices of 'caraguata' from Argentina, with the same note types identified at all localities. The introduction (Fig. 6A–B), full song (Fig. 6C–E) and calls (Fig. 6F–H) conform to the normal individual variation in structure

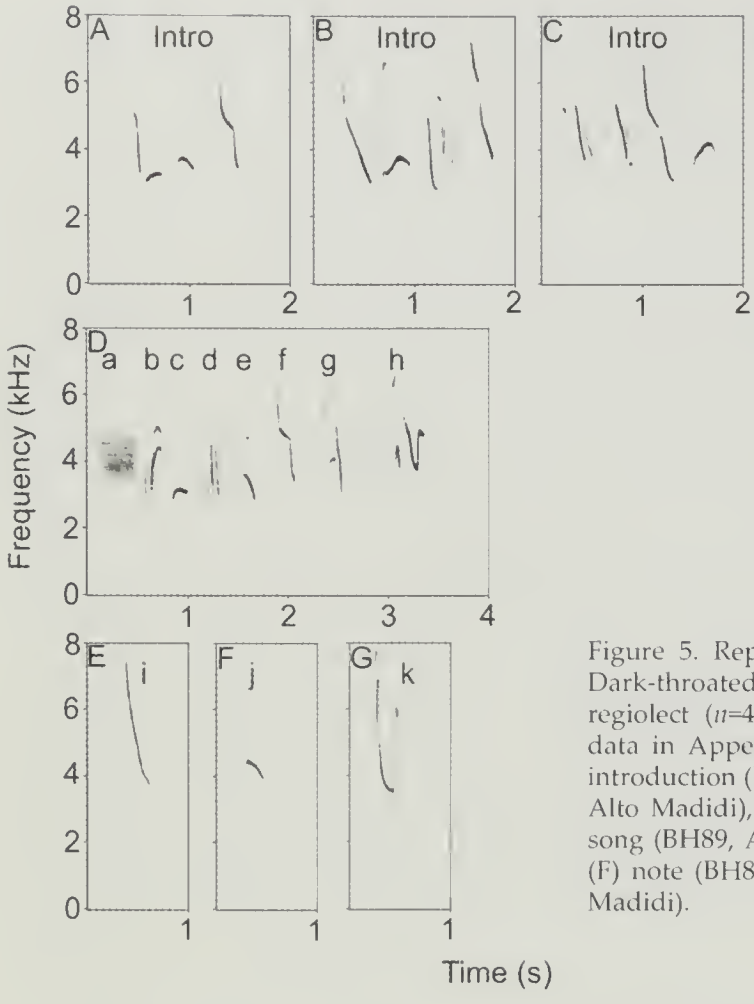

Figure 5. Representative sonograms of vocalisations of Dark-throated Seedeater *Sporophila ruficollis*, Alto Madidi regiolect (n=4). Numbers in parentheses correspond to data in Appendix 1, locality not mapped in Fig. 2. (A) introduction (BH89, Alto Madidi), (B) introduction (BH90, Alto Madidi), (C) introduction (BH91, Alto Madidi), (D) song (BH89, Alto Madidi), (E) note (BH88, Alto Madidi), (F) note (BH88, Alto Madidi), and (G) note (BH88, Alto Madidi).

TABLE 3

Note types and % of individual males whose songs included relevant notes in Dark-throated Seedeater *Sporophila ruficollis* (Mesopotamia and Apolo-Madidi regiolects, Figs. 4–5), the 'caraguata' form (Fig. 6) and Chestnut Seedeater *S. cinnamomea* (1991–93 and 2003–07 chronolects, Fig. 7). Note names do not imply homology, except when comparing *S. ruficollis* from Mesopotamia and the 'caraguata' form. Sample size (n) in parentheses.

	Intro.	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s
S. ruficollis Mesopotamia, 2003–08 (78)	66.7	66.7	65.4	61.5	57.7	59	60.3	60.3	57.7	57.7	44.9	47.4	25.6	50	41	35.9	20.5	16.7	29.5	38.5
S. ruficollis Apolo Madidi, 2003 (4)	75	50	25	25	25	25	50	25	25	25	25	50								
'caraguata' Mesopotamia, 2007 (3)	66.7	100	100	100	100	100	100	100	100	100	100	100	100	66.7	66.7	66.7	100	66.7	100	100
S. cinnamomea, 1991–93 (4)		100	100	100	75	75	100	75	75		75									
S. cinnamomea, 2003–07 (20)		65	65	55	65	65	65	65	65	55	65	50								

of the Mesopotamia regiolect of *S. ruficollis* (Fig. 4A–H). Hence, there are no consistent vocal differences between 'caraguata' and *S. ruficollis*. Given the conservatism in the basic vocal structure in *S. ruficollis* from the Mesopotamian grasslands (n=78), we suggest that

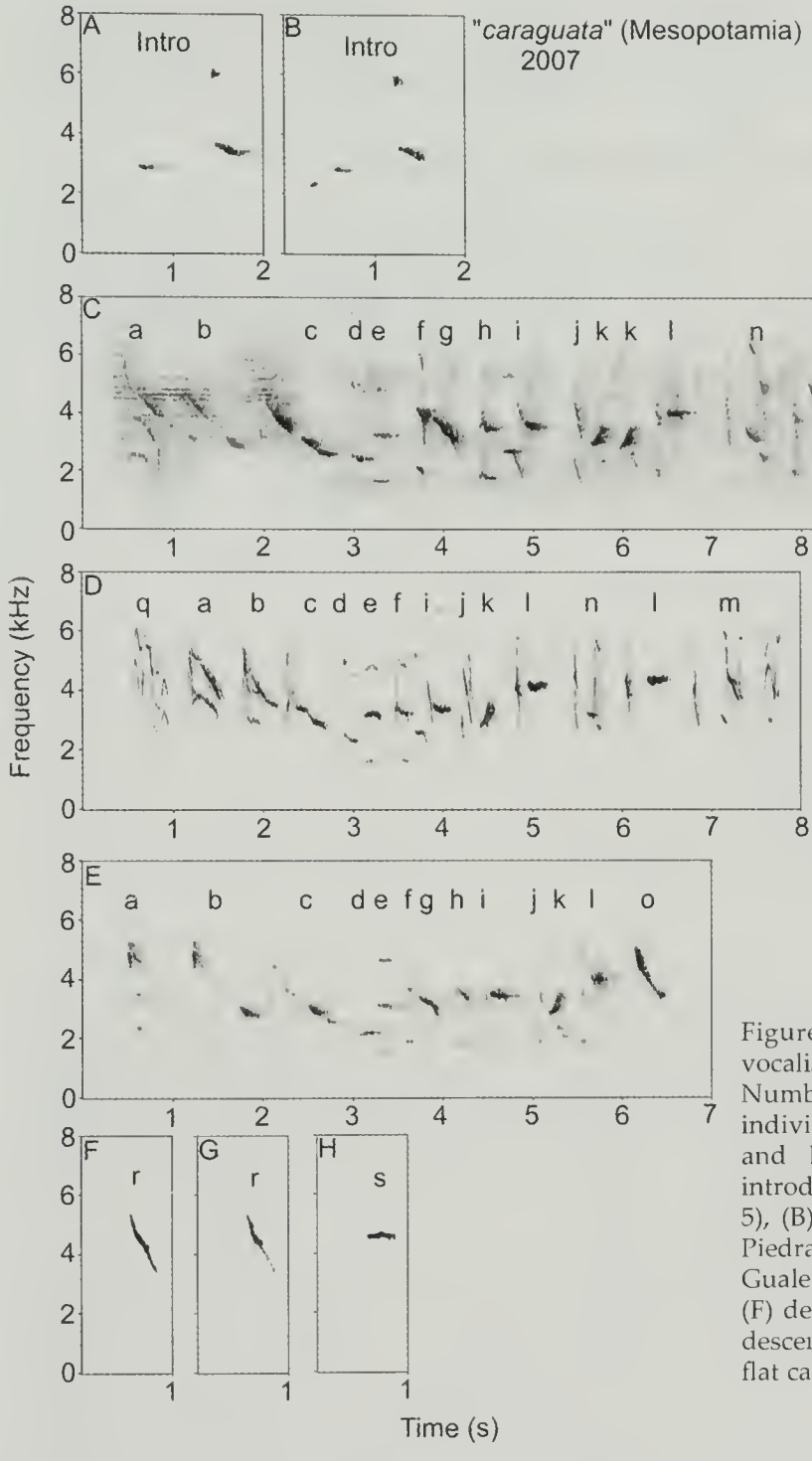

Figure 6. Representative sonograms of vocalisations of the 'caraguata' form (n=3). Numbers in parentheses correspond to individuals in Appendix 1, locality name and locality number as in Fig. 2. (A) introduction with two notes (1, Las Piedras–5), (B) introduction with three notes (1, Las Piedras–5), (C) song (2, Ibicuy–2), (D) song (3, Gualeguaychú–5), (E) Song (1, Las Piedras–5), (F) descending call (3, Gualeguaychú–5), (G) descending call (1, Las Piedras–5), and (H) flat call (2, Ibicuy–2).

our recordings of 'caraguata' (n=3 individuals) are probably representative of the form in this region. A fourth male 'caraguata' from Perdices (not tape-recorded), responded aggressively to playback of *S. ruficollis* and its song was identical (J. La Grotteria *in litt.* 2010). Trappers reported that all 'caraguata' (n=12) were attracted to the voice of *S. ruficollis* and that they ignored voices of species such as *S. palustris* and *S. cinnamomea*, which were also used in trapping attempts.

Main song and calls of *S. cinnamomea* do not resemble those of *S. ruficollis* or 'caraguata' (Figs. 4–7, Table 3). None of the notes in the repertoire of *S. ruficollis* and 'caraguata' was present in the songs of *S. cinnamomea*, for which 11 diagnostic notes were identified (Fig. 7, Table 3). The last segments of the full song of *S. cinnamomea* were seldom recorded and could not be characterised. No geographical variation was detected but old recordings of *S. cinnamomea* differ from modern recordings (*cf.* Areta 2008).

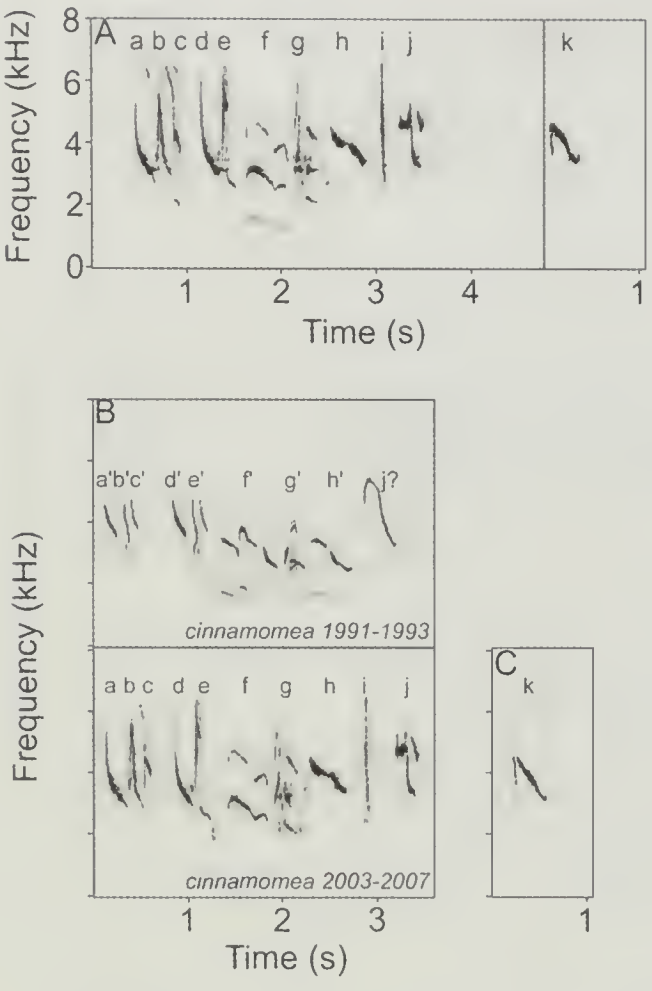

Figure 7. Representative sonograms of vocalisations of Chestnut Seedeater *Sporophila cinnamomea* (*n*=24). Numbers in parentheses correspond to individuals in Appendix 1, locality name and locality number as in Fig 2. (A) initiation and middle portion of song and call of *S. cinnamomea* in 2003–07 depicting delimitation of note types; song (5, Rincón del Socorro–15) and call (5, Rincón del Socorro–15), (B) initiation and middle portion of song in 1991–93 (above, AJ21, Mercedes–14), and in 2003–07 (below, 5, Rincón del Socorro–15), and (C) call in 2003–07 (14, Lorenzo Geyres–24). Inferred homologies are described using apostrophes ('), and interrogation mark denotes doubt regarding homology.

Hypothesis testing.—The hypothesis that the 'caraguata' form is a valid species is rejected using song and habitat data, because there are no species-specific notes in their songs and no species-specific habitat (Table 1). No notes in the song of 'caraguata' distinguish it from *S. ruficollis* (Figs. 4 and 6, Table 3) and the two forms are syntopic. In contrast, *S. cinnamomea* differs both in voice (Figs. 4–7, Table 3) and preferred habitat from 'caraguata' and *S. ruficollis*, exemplifying expected species-specific differences in habitat and vocalisations between closely related species.

The hypothesis that 'caraguata' is a hybrid between *S. ruficollis* and *S. cinnamomea* is partially rejected by both vocal and habitat data (Table 1). Because there is no evidence of intermediacy in the vocalisations of 'caraguata' between its putative parental forms *S. ruficollis* and *S. cinnamomea*, the mixed-voice prediction is rejected (Figs. 4–7, Table 3). However, if songs were inherited or learned exclusively from males, similarities between songs of *S. ruficollis* and 'caraguata' would be expected even if the latter is a hybrid. If 'caraguata' is of hybrid origin and songs are learned, evidence suggests that *S. ruficollis* is always the paternal form. Habitat overlap between the proposed parental forms *S. cinnamomea* and *S. ruficollis* is limited, but sufficient to permit hybridisation. However, 'caraguata' was never found in the undulating grassland habitat of *S. cinnamomea*. Thus, voice and habitat suggest that male *S. cinnamomea* might not be important in the origin of 'caraguata'. None of this hypothesis' predictions was fully supported by our results.

The hypothesis that 'caraguata' is a colour morph of *S. cinnamomea* is rejected based on vocal and habitat data (Table 1). The songs of 'caraguata' and *S. cinnamomea* differ in note structure, pace and duration (Figs. 6–7, Table 3). Furthermore, there is little habitat overlap between 'caraguata' and *S. cinnamomea*, and 'caraguata' was never found in the preferred habitat of *S. cinnamomea*.

That 'caraguata' is a colour morph of *S. ruficollis* is supported by vocal and habitat data (Table 1). The note repertoire of 'caraguata' is a subset of that of *S. ruficollis* (Figs. 4 and 6, Table 3). Both 'caraguata' and *S. ruficollis* prefer caraguatal-cardal habitat.

Discussion and Conclusion

Systematics of the 'caraguata' form.—The rare 'caraguata' form coincides in vocalisations and preferred habitat with the common *S. ruficollis*, providing evidence that they are syntopic colour morphs (Table 1). No undoubtedly valid species of *Sporophila* is extremely rare in adequate habitat (Areta 2008). Consequently, we interpret the extreme rarity of 'caraguata' as further undermining the valid species hypothesis. However, rarity is consistent with both the presence of a morph or hybridisation events. Although it might be argued that 'caraguata' represents older individuals of *S. ruficollis*, the presence of a dark collar in presumed young 'caraguata' males and the existence of old *S. ruficollis* without a dark collar eliminate this possibility.

The case of the dark-collared and rufous-backed 'caraguata' form as a morph of the dark-throated and grey-backed *S. ruficollis* mirrors that of the exceedingly rare white-collared and rufous-backed *S. zelichi*, which was suggested to be a morph of white-throated and grey-backed *S. palustris* based on striking similarities in voice, habitat, and patterns of rarity, spatial and temporal distribution (Areta 2008). It could be argued that 'caraguata' is a morph of *S. zelichi*, as they differ only in the colour of the collar (dark in the former, white in the latter). However, vocalisations and habitat use differ markedly between 'caraguata', which inhabits dry grassland, and *S. zelichi*, which inhabits marshes and wet grasslands (Areta 2008, this work), rejecting the idea that they are morphs of the same species.

Despite the occurrence of hybrid *Sporophila* (Lordello 1957, Sick 1963, 1997; pers. obs.), testing the hybridisation hypothesis is difficult (de las Casas 2004, Areta 2008). The only case of presumed hybridisation between a female assigned to *S. ruficollis* and a male *S. cinnamomea* was in captivity, but the resultant sex and plumages of the hybrids were not described (Sabel 1990). While the presumed hybrid *S. ruficollis* × *S. cinnamomea* reached normal size, captive hybrids between a female *S. ruficollis* and a male *S. palustris* did not, presumably because they did not survive to adulthood (Sabel 1990). Although highly instructive, promissory and enlightening as to inheritance and ontogeny of plumage, the occurrence of hybridisation in captivity cannot be assumed to demonstrate its occurrence in nature (e.g., Sick 1962, Grant & Grant 1992). Moreover, given the lack of critical data regarding the identification of females involved in Sabel's (1990) crossings, the data should be interpreted cautiously. Data presented here do not eliminate the hybridisation hypothesis; however, the limited habitat overlap and lack of shared vocal characters of 'caraguata' with *S. cinnamomea* are inconsistent with hybrid origin (Table 1). Our 'caraguata' specimen, live individuals and observations agree in colour intensity with *S. ruficollis*, but never approach the chestnut saturation in male *S. cinnamomea* (see below), providing further evidence against the hybrid hypothesis.

Because *S. ruficollis* is more widespread than *S. cinnamomea*, further testing of the hybridisation hypothesis and colour morph hypothesis II is possible. The hybridisation hypothesis predicts that 'caraguata' should occur only where *S. cinnamomea* is also present (assuming philopatry of hybrids), while colour morph hypothesis II predicts that 'caraguata' could potentially appear anywhere within the range of *S. ruficollis*, independent of the presence of *S. cinnamomea*. Measurements do not differ consistently between *S. ruficollis*, *S. cinnamomea* and 'caraguata', and do not appear useful in elucidating the systematics of the group.

Geographic variation in the vocalisations of *S. ruficollis* was detected in this study, with two widely allopatric regiolects (Mesopotamia and Alto-Madidi), but 'caraguata' was found only within the area of occurrence of the Mesopotamia regiolect, and sings like birds there. Both *S. ruficollis* and presumed 'caraguata' males from Corrientes, Argentina, should be tape-recorded for comparison as their voices might differ from those elsewhere (pers. obs.). The few recordings of the apparently isolated and resident population of *S. ruficollis* in the Apolo-Madidi savannas (Bolivia) exhibit several differences from those from Argentina and Uruguay, and merits further study. Although imitation has been reported for several *Sporophila* not closely related to the capuchinos—Rusty-collared Seedeater *S. collaris* (Moschione 1989; pers. obs.), Grey Seedeater *S. intermedia* (Thomas 1996) and Plumbeous Seedeater *S. plumbea* (Sick 1997; pers. obs.)—we lack evidence of vocal mimicry in any capuchino (JIA unpubl.: *n*=230 individuals of all species in the *ruficollis* group). Moreover, the concerted vocal changes over time in *S. palustris*, and its presumed morph *S. zelichi*, suggest a common mechanism of restriction in vocal learning (Areta 2008). Unfortunately, we lack comparable recordings of *S. ruficollis* and 'caraguata' through time to further test this hypothesis.

Although 'caraguata' would have been considered a species using the traditional colour-based species delimitation criteria in capuchinos, the evidence does not support this (Table 1). The concept of morph (Huxley 1955, Gray & McKinnon 2006) implies that exclusive assortative mating within a species is not strictly dependent upon the presence of a single plumage pattern (i.e., *ruficollis* females would be more attracted to both *ruficollis* and 'caraguata' males over hetero-specific plumages). This underscores the importance of not assuming *prima facie* that diagnosable plumage traits directly represent discrete biological entities. The association of complementary plumage and vocal traits presumably provides key species-specific cues for recognition (Irwin & Price 1999, Price 2007), but the precise mechanisms through which plumage pattern and voices are involved in recognition or the effect of mis-associated male plumage and vocal features on female choice (e.g., a *S. cinnamomea* plumaged male with a *S. ruficollis* voice) have not been explored to date in capuchinos. Finally, if 'caraguata' is a morph product of a rare alelle, the commonly traded *S. ruficollis* should be protected to ensure its long-term persistence.

Systematics of S. ruficollis.—Because our data are more consistent with the notion that 'caraguata' is a morph of *S. ruficollis*, we now discuss the systematics and taxonomy of *S. ruficollis*. *Sporophila ruficollis* Cabanis, 1851, was described from a young male presumably from Montevideo (Uruguay), based on the manuscript / label name *Fringilla ruficollis* assigned by Lichtenstein to a specimen in Berlin. Sclater (1871) and Sharpe (1888) considered *S. ruficollis* to be a young *S. hypoxantha*. The link between the type of *S. ruficollis* (grey cap, chocolate throat, pale creamy underparts and brownish upperparts) and adult males was only elucidated by Hellmayr (1904, 1938) who subsumed *Spermophila plumbeiceps* Salvadori, 1895, in *S. ruficollis*. Hellmayr (1904, 1938) discussed plumage variation in *S. ruficollis*, while casting doubt on the validity of the type locality, albeit without rationale. However, Lichtenstein (1854: 46) reported a specimen from 'Brasilien' held in Berlin, presumably the type that Hellmayr (1904, 1938) examined. Unfortunately, the type of *S. ruficollis* cannot be found in the Museum Heineanum (Halbsertadt: B. Nicolai *in litt.* 2009) or Museum für Naturkunde (Berlin: S. Frahnert *in litt.* 2009), and appears to be lost.

Our data on *S. ruficollis* based on specimens and field observations agree with those previously published on the great variability in pigment saturation in the species (Hellmayr 1904, 1938, Meyer de Schauensee 1952, 1966). Most important, for taxonomy, are the variations in throat and belly colour. In presumed adult males, the colour of the throat varies from dark rufous to black, while the belly is pale to dark rufous. This suite of variants

occurs in the same habitats in large geographical areas where no other male capuchino is found, supporting its purely individual nature. Our field observations suggest that darker individuals are older males (Hellmayr 1904). However, dark and pale siblings of the same age occur in captivity (R. Tato pers. comm.), suggesting that darker pigmentation is a function of both age and individuality.

Short (1969a: 219) suggested that *S. ruficollis* might be a colour morph of *S. hypoxantha*, and contested that 'Both dark and light throated forms are found side by side in the same wet pampas of Corrientes, and probably elsewhere'. However Hartert & Venturi (1909: 175), stated that *S. ruficollis* nests 'in the little bushes . . . found here and there in the dry and elevated fields', and that *S. hypoxantha* 'nests amidst the short grasses found in areas with marsh ant nests'. Short (1975) added that *S. ruficollis* and *S. palustris* are colour morphs of *S. hypoxantha*, although he noted that field studies were needed to clarify this, and he found habitat of parental forms and presumed hybrids an important taxonomic indicator (Short 1969b: 85). *S. ruficollis* (this work) and *S. hypoxantha* (Hartert & Venturi 1909, Areta 2010) differ in voice and preferred habitat, whilst differences in habitat, vocalisations and distributions suggest species-level differences for *S. ruficollis* and *S. palustris* (Areta 2008, this work). Thus, there is no support, on natural history grounds, to consider *S. hypoxantha*, *S. ruficollis* and *S. palustris* as colour morphs of the same species (but see below for an alternative polymorphism hypothesis).

Sabel (1990) suggested that *S. zelichi* is a morph of *S. ruficollis*, based on unstated evidence, whilst Lewis (1997) proposed, based on limited mtDNA evidence (cytochrome-*b* 350bp, pair-wise distance 1.3%) that *S. ruficollis* is more closely allied to *S. zelichi* than to other capuchinos, and that they could be 'colour phases' of the same species. The data presented here, together with those of Areta (2008) reject this idea: *S. zelichi* differs in vocalisations and preferred habitat from *S. ruficollis*, aside from their very different plumages. Finally, Armani (1985) illustrated a male 'caraguata' as representative of *S. ruficollis*, which we consider erroneous (see Results).

In sum, our results support treatment of *S. ruficollis* as a valid species, with the inclusion of the rare 'caraguata' form as a colour morph. Because females have to date proved indistinguishable among all species in the *ruficollis* group we cannot evaluate whether there are also female morphs. Until this question is elucidated, *S. ruficollis* should be considered a male-dimorphic species.

Radiating capuchinos?—The lack of genetic structure in the *ruficollis* group (Lijtmaer *et al.* 2004, Kerr *et al.* 2009) conflicts with the clear differences in plumage, vocalisations and habitat use (Areta 2008, 2010, this work). This apparent incongruence suggests: (1) recent divergence not yet reflected in the studied genes; or (2) the existence of an ultra-polymorphic species with varying degrees of isolation between different forms in the *ruficollis* group (Areta 2008). Under the second hypothesis, female capuchinos may mate freely with all male forms, erasing any genetic distinctiveness, while the diagnostic features of voice and habitat preference of males could be cultural traits over-imposed on a common gene pool. This hypothesis differs from the simple colour morph hypothesis proposed by Short (1969b, 1975) in which birds merely differ in plumage.

Habitat imprinting could play a crucial role in the generation and maintenance of habitat preferences in birds (Davis & Stamp 2004, Beltman & Haccou 2005) which could result in assortative mating within preferred habitats. In turn, magnitude of ecological divergence can also play an important role in reproductive isolation independent of divergence time between forms (Funk *et al.* 2006, Nosil *et al.* 2009). Sick (1967: 309) stated that 'habitat segregation—which prevents the meeting of potential mates—represents, in the case of seedeaters, the most important isolating mechanism'. Given the contrast between the

scant genetic differentiation and the habitat divergence in these forms, habitat segregation through imprinting is thought to play a key role in the evolution of capuchinos (Areta 2010). Two issues are worth mentioning. First, preferred habitats often occur side by side in the Mesopotamian grasslands of Argentina and in Uruguay, permitting potential mixing between males and females of most forms spatially and temporally. Second, capuchinos forage and migrate in mixed-species flocks. These can be misleading when evaluating breeding habitat, because habitat use by mixed flocks does not necessarily correspond to the preferred habitat of breeders and territorial males (pers. obs.). For example, Azara (1802) was confused when he included *S. bouvreuil pileata*, *S. ruficollis*, *S. palustris* and probably even a young *S. cinnamomea* in the 'Pico Grueso Variable'. He collected birds that differed in body-feathers but not in wing pattern in the same flocks, and erroneously considered them a single highly variable species.

Early stages of evolutionary radiations are characterised by 'fuzzy' species borders with frequent hybridisation (Price 2007, Grant & Grant 2008). Capuchinos, especially the *ruficollis* group, might represent a very early evolutionary radiation, with the ecologically differentiated forms capable of hybridising but rarely producing fit hybrids and back crosses. Differentiation presumably occurred with very little genetic divergence, simple changes in colour patches of male plumages, divergence in habitat and voices, but little morphological change in size and shape and virtually no differences among females (Areta 2010). The existence of several new forms of capuchinos in the process of being described will provide data to further test these ideas.

The taxonomic conundrum.—The 'caraguata' form is not a species under the Recognition Species Concept (or the Biological Species Concept and probably also under some versions of the Phylogenetic Species Concept; see Eldredge 1995, Haffer 1997). Although most evidence supports it being a colour morph of *S. ruficollis*, a slight possibility exists that it is a hybrid. Clearly, this situation is conflictive, since traditional taxonomic concepts and methods do not suffice to provide a name or category to accurately describe this situation (Selander 1971, Grant & Grant 2006, 2008).

If we explicitly consider 'caraguata' a morph of *S. ruficollis*, then 'caraguata' is an infra-subspecific name according to the *International code of zoological nomenclature* (ICZN 1999). Names expressly proposed to denote infra-subspecific entities are not available under the rules of the ICZN, are excluded from the species group and not regulated by the ICZN (1999; Art. 45.6). Although the ICZN does not preclude the erection of names for taxa of hybrid origin (Arts. 1.3.3, 17.2 and 23.2), it would be confusing (if 'caraguata' subsequently proves to be a hybrid) to erect a new species name for this peculiar systematic situation.

We have referred to this diagnostic plumage as 'caraguata' or the 'caraguata' form. An alternative would be to employ an informal binomial, i.e. *Sporophila 'caraguata'*, to denote its uncertain taxonomy, as used elsewhere in *Sporophila* (Olson 1981). However, our referees argued strongly against this, despite its usefulness to accommodate the situation of both *S. 'zelichi'* and *S. 'caraguata'* (Areta 2008, 2010). We strongly recommend acknowledging the uncertainty regarding hybrid origin by referring to 'caraguata' as either *Sporophila 'caraguata'* or the 'caraguata' form, and suggest caution with the use of alternatives directly acknowledging its morph status as *Sporophila ruficollis* morph 'caraguata' or *Sporophila ruficollis* dark-collared morph.

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APPENDIX 1: recording localities, dates and identification of voices

Localities are shown in Fig. 3. Numbers in [ ] indicate number of individuals per locality and those in ( ) indicate number assigned to each bird in JIA database. All recordings by JIA except those by AJ = Alvaro Jaramillo, BH = Bennett Hennessey, MP = Mark Pearman, RF = Rosendo Fraga. All recordings of 'caraguata' are from birds in captivity.

S. ruficollis [82] **Mesopotamia regiolect** [78]. Argentina. Entre Ríos: Arroyo Baru [8] (4–11), Larroque-Urdinarrain [11] (20–27, 38–40), San Salvador [6] (12–17), Gualeguaychú [5] (33–37), Estancia La Marita [4] (1, 2, 18, 19), Puerto Liebig and Arroyo Caraballo [1] (3). Santa Fé: Sauce Viejo [5] (28–32). Buenos Aires: Saladillo [10] (41–50). Uruguay. Dpto. Paysandú: Lorenzo Geyres-Quebracho [26] (51–76), Queguayar [2] (77, 78). **Alto Madidi regiolect** [4]. Bolivia. Dpto. La Paz: Apolo-Madidi [4] (BH88–91).

'caraguata' [3] Argentina. Entre Ríos: Las Piedras [1] (1), Ibicuy [1] (2), Gualeguaychú [1] (3).

S. cinnamomea [24] Argentina. 1992–93: Corrientes: Mercedes [2] (AJ21, AJ22), Caza Pava [1] (MP24). Entre Ríos: Parque Nacional El Palmar [1] (MP23). 2003–07: Corrientes: Estancia El Socorro [9] (1–5, 7–10), Mercedes [1] (1), Colonia Pellegrini [2] (11,12). Entre Ríos: Gualeguaychú [1] (13). Uruguay. 2003–07: dpto. Paysandú: Lorenzo Geyres [5] (14–18), San Javier/Río Negro [1] (RF19), Villa Soriano/Río Negro [1] (RF20).

APPENDIX 2: localities at which habitat use data were obtained

Localities are shown in Fig. 3. Numbers in [ ] indicate number of individuals per locality.

S. ruficollis [110] Argentina. Corrientes: Colonia Pellegrini [5], Estancia El Socorro [3]. Entre Ríos: Gualeguaychú [14], Larroque-Urdinarrain [15], Arroyo Baru-San Salvador [27], Estancia La Marita [3]. Buenos Aires: Saladillo [12]. Santa Fé: Sauce Viejo [4]. Uruguay. Dpto. Paysandú: Lorenzo Geyres-Quebracho [23], Queguayar [4].

'caraguata' [14] Argentina. Entre Ríos: Gualeguaychú [10], Ibicuy [1], Las Piedras [1], Arroyo Ñancay [1], San Juan Poriahú [1].

APPENDIX 3: specimens examined

S. ruficollis. AMNH: 156535, 514650–653, 514656–662, 789493, 798446, 798486–492, 798494, 798495, 798497–507, 798510–519, 799118, 810666, 825230. FML: 2123, 2141, 2176, 8798, 9603, 9770, 9793–95, 9801–02. MAS: 4749. MNHN: 5781, 5782, 5784, 5785, 6111, 6113, 6114, 6116.

'caraguata'. MLP: 14044. See Morphology for two additional live specimens.

S. cinnamomea. AMNH: 320211, 320653, 320654. MNHN: 6022, 6031, 6108, 6119, 6121. Museo Ornitológico de Berisso: no number assigned.

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Notes on the breeding of high-Andean birds in northern Ecuador

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Summary.—The breeding biology of tropical birds is poorly known, especially in the high Andes. We present observations on the nesting of 76 species of birds from the Ecuadorian highlands (above 2,700 m). For many of these species this is the first breeding information available for Ecuador. We present detailed accounts for several species, including the first described nests of Plain-capped Ground Tyrant *Muscisaxicola alpina* and Chestnut-winged Cinclodes *Cinclodes albidiventris*.

The studies of Marchant (1959, 1960) then Best *et al.* (1993, 1996), Rasmussen *et al.* (1996) and Greeney *et al.* (2010) in southern Ecuador, and other recent papers focusing on the north-west (e.g. Marín & Carrión 1991, 1994, Greeney & Nunnery 2006, Solano-Ugalde *et al.* 2007), east (Greeney *et al.* 2004, Greeney & Gelis 2007, 2008, Greeney & Merino 2007), and elsewhere (Kiff *et al.* 1989), have begun the monumental task of documenting breeding seasons at a national level. Much work remains, however, and notably neglected are the Andes above 2,700 m (but see scattered records in Lönnberg & Rendahl 1922, Hilty & Brown 1986, Marín & Carrión 1994, Greeney & Martin 2005, Cisneros-Heredia 2006, Solano-Ugalde 2008).

Here we present 343 observations on the breeding activity of 76 species of birds, collected over the last seven years, predominantly from the vicinity of Papallacta, prov. Napo (00°19'S, 78°12'W) (PP) at various elevations. Also in Napo we studied nests at Guango Lodge (00°22'S, 78°04'W) (GU). In addition we gathered information from the areas in and around Quito, prov. Pichincha (QU), Micacocha, prov. Napo (00°30'S, 78°14'W) (MC), Otavalo, prov. Imbabura (OT), Yanacocha, prov. Pichincha (00°06'S, 78°35'W) (YA) and the slopes of Cotopaxi Volcano, prov. Cotopaxi (00°38'S, 78°27'W) (CO). Observations were made opportunistically during the course of other field work. In conjunction with past and future observations the data presented here comprise a significant contribution to our knowledge of birds from the highlands of Ecuador.

For brevity, we have not exhaustively reviewed the breeding literature for each species, instead we indicate only other Ecuadorian records or particularly relevant works. We use the following abbreviations: (B) building, (I) incubating, (N) nestlings, (F) fledglings, (AN) active nest at unknown stage, (CF) adult carrying food, and (CM) carrying nesting material but nest unseen.

Species accounts

CHESTNUT-WINGED CINCLODES *Cinclodes albidiventris*

We found all nests at PP, at elevations of 3,900 to 4,230 m. We discovered the first nest on 29 May 2003, at which time we noted only that at least one adult was repeatedly entering a nest tunnel. Subsequently, on 22 November 2003, we discovered a single nest with two nestlings. In 2004 we found three active nests. One was incubating two fresh, all-white eggs (26.7 × 20.2 and 26.8 × 20.2 mm) on 22 October. After the adult was flushed from the nest, it returned with fresh moss in its bill, indicating that this species continues to add material

to the nest during incubation. The other two nests contained nestlings on 1 August and 17 October, respectively. At the two nests where we were able to examine the nestlings, there was one in each. At one nest an adult brought the nestling a brown lepidoptera pupa *c.*3 cm long. In 2005 we observed five nests. The first contained two nestlings on 27 August 2005 and the second a single cold, all-white egg at 06.45 h on 30 September. At 16.45 h on 1 October, there was still only one egg, but a second egg was laid before 07.00 h on 2 October. This indicates that the eggs were laid more 34 hours apart. After 12 days of incubation we found the nest and eggs destroyed in front of the nest entrance. A third nest contained two all-white eggs on 1 October. Eight days later the nest was empty and we found broken eggshells in front of the nest. On 4 October, at 07.30 h, we found a nest with a single cold, all-white egg. Again, at least 35 hours passed before we found a second egg. These eggs were incubated for at least 17 days until we ceased monitoring the nest. On 18 October we found an additional nest with an adult incubating two all-white eggs. In 2006, we observed one individual excavating a nest tunnel on 31 July, nests with two eggs on 23 and 29 September, and nests with nestlings on 29 August, 14 October and 1 November. We subsequently found nests with nestlings on 26 October and 6 December 2007, and 17 January 2008, as well as observing an adult carrying rabbit fur into a freshly excavated tunnel on 26 October 2008. All nests were neat, shallow cups of rootlets lined first with pale green moss and lichens, and then sparsely with feathers. One nest measured 16 cm wide by 5.5 cm tall outside and 6.5 cm wide by 3.5 cm deep inside. Although there are brief mentions of the use of burrows in this species by Taczanowski (1884) and Crawshay (1907), this appears to be the first complete description of the nest for this widespread and common species.

STOUT-BILLED CINCLODES *Cinclodes excelsior*

We found most nests at PP, at elevations of 3,950 to 4,300 m. On 17 October and 5 December 2004 we found two nests with two nestlings each. We found three nests in 2005. On 22 August we found a nest at which an adult was adding material to the empty nest cup. Eventually, two all-white eggs (29.6 × 21.8 and 29.6 × 22.4 mm) were laid before 2 September. Both eggs hatched before 24 September and the nest was empty 14 days later. While the nest contained nestlings, we observed an adult arriving with material to add to the nest. On 4 October we found a nest with an adult incubating two all-white eggs. They were incubated for at least 17 days before we ceased monitoring. Finally, on 16 October we found a second nest with an adult incubating two all-white eggs.

At PP we found two additional nests during incubation on 10 November 2006, and nests with nestlings on 18 October 2006, 26 October 2007 and 24 and 26 October 2008, an active nest on 13 December 2009, and an adult feeding a young fledgling on 6 December 2007. We found three additional nests with nestlings at MC on 30 December 2007 (two nests) and 6 December 2009. All nests were built inside earthen tunnels in road cuts. They were all constructed entirely of pale yellow straw-like material. Two nests measured 15 cm and 22 cm wide by 7.5 cm and 7 cm tall outside, with unlined egg cups measuring 8.0 cm and 9.5 cm in diameter by 5 cm and 4 cm deep, respectively. One was built atop an older, partially decomposing nest, probably of the same species. Our nest and egg descriptions match those from the only other study of the nesting of this species (Graves & Arango 1988).

ANDEAN TIT-SPINETAIL *Leptasthenura andicola*

We found all nests at PP, at elevations of 3,900–4,230 m. The first contained two nestlings (9.7 g and 9.4 g) on 5 December 2004. On 13 December the nest contained only a single nestling which weighed 16.6 g. This nest was nestled into a cavity at the top of a road cut 2.3 m up. The cavity was formed by a cushion plant (Asteraceae) overhanging the bank, with

the top, front and bottom composed of the plant and the back composed of bare dirt. The nest was an incomplete ball, with the top and back not completely formed, relying instead on the bank and cushion plant. The outside of the ball was composed of an estimated 90% grass stems and small sticks, and 10% moss. Inside, the nest was densely lined with *c.*70% mammal fur, 20% *Puya* sp. (Bromeliaceae) seed down and 10% feathers. The lining also included a long piece of blue plastic string. Outside dimensions of the ball were 14.5 cm tall by 11.5 cm wide, by 11 cm front to back. Inside, the chamber was 7.5 cm tall overall, with a cup 4.5 cm wide by 3 cm deep. All other nests seemed similar to this one, but we did not examine them closely. Of nine nests, two were built inside earthen tunnels, presumably excavated by other species, with their entrances <10 cm from the exterior of the hole. The remaining seven nests were built inside natural cavities created by overhanging vegetation beside a rock or dirt bank. In 2005, we found four nests under construction on 22 August, 24 and 26 September, and 12 October. Additionally, we found two nests with incubation underway on 26 September, one on 29 September and one on 20 October. All eggs we examined were immaculate white and seven eggs had mean measurements of 20.1 ± 0.8 by 15.4 ± 0.6 mm (range = 19.4–21.8 × 14.9–16.6 mm). At 13 nests clutch size was two. At three nests we observed both adults were building, and at two nests both adults provisioned the nestlings. At one nest the second egg was laid between 06.15 h and 12.15 h. At two nests eggs were laid at least 72 hours apart and at one at least 48 hours apart. Eggs at two nests were incubated for at least 16 days before we ceased monitoring them or they hatched. At one nest, on the day the second egg was laid, we later found it broken on the ground in front of the nest. The adult, however, continued to incubate the remaining egg, which proved infertile. At three nests, both nestlings hatched on the same day. At six nests where we determined their fate, one fledged two young and five failed (four with eggs, one with nestlings).

In 2006 we found ten additional nests. We observed nests under construction on 23 September and 14 October. We found nests with incubation underway on 14, 18 (n=2) and 23 October, as well as two nests on 10 November. On 10 November we also found two nests, each with two nestlings. We found an additional nest with eggs on 26 October 2007, nests with nestlings on 24 October 2008 and 9 December 2009, and one active nest of unknown stage on 13 December 2009.

PLAIN-CAPPED GROUND TYRANT *Muscisaxicola alpina*

Near PP, at 4,275 m, on 23 September 2006 we flushed an adult from a nest containing two eggs. The eggs were white with cinnamon flecking heaviest at the larger end. They measured 27.6 × 18.8 mm and 27.1 × 18.7 mm, and weighed 4.69 g and 4.71 g, respectively. Six days later we weighed the eggs again, at which time they had lost weight reflecting a daily mass-loss of 1.3% and 1.1%, respectively. On 11 October the nest was empty but intact. The nest was an open cup on a thin, well-sheltered rock ledge 1.4 m above ground and 2.1 m below the top of the cliff. The cup consisted of three layers, an outer layer of loose moss and thin rootlets, a dense inner lining (3 cm) of dark, fibre-like lichens, and a thin, innermost layer of hair and feathers. Internally the cup was round and measured 7.0 cm in diameter by 5.5 cm deep. Externally the nest was slightly elongated parallel to the cliff and measured 15 cm wide by 13 cm front to back. Supporting the cup on the slightly irregular rock ledge was a 10-cm lip of moss extending forward from the nest to the edge of the ledge. In addition to this nest, on 11 October 2008 at MC (3,960 m) we observed two adults carrying material into the eaves of an abandoned house. This appears to be the first nest description for this species.

PLUMBEOUS SIERRA FINCH *Phrygilus unicolor*

On 17–18 October 2004, we found two nests, one with one egg and one with two, at PP, at 4,100 m, and MC, respectively. In 2005 we found a nest with two eggs on 24 October at PP, at 4,000 m. In 2006 we found two nests on 3 August at CO, both at 3,800 m. One contained a single undeveloped egg and the second contained two partially developed eggs. At PP in 2006, at elevations of 4,000–4,200 m, we found nests with eggs on 14 October, 18 October (n=3) and 1 November, and nests with nestlings on 18 October and 1 November. In 2007 we observed an adult carrying food on 26 October at PP (4,000 m), and found a nest with nestlings on 30 December at MC (4,000 m).

All eggs were blue with dark red-brown flecking and speckling, heaviest at the larger end and usually forming a ring. Mean (± SD) measurements of six eggs were 24.7 ± 0.7 × 16.6 ± 0.8 mm (range = 24.0–25.8 × 15.7–17.5 mm). All nests were bulky open cups comprising short twigs and grass stems mixed with moss. All were densely lined with varied soft materials including feathers, *Puya* sp. seed down, mammal fur, sheep wool and horse hair. Four nests were nestled into bunch grass clumps, and one was in a multiple fork of an unidentified Asteraceae. Mean nest height was 0.9 ± 0.4 m. Mean measurements for four nests were: outside width 13.6 ± 2.2 cm; outside height 9.8 ± 0.5 cm; inside diameter 6.3 ± 0.3 cm; inner cup depth 4.4 ± 0.3 cm. One nest was built atop an old nest, seemingly of the same species, causing the entire structure to be 17 cm tall. This species' nest and eggs were first described by Armani (1985) but few other data are available on its breeding behaviour.

In addition, we recorded the following information: **Silvery Grebe** *Podiceps occipitalis*, 22 July 2008 MC 3,900 m (AN), five nests with adults sitting, 17 November 2008 MC 3,900 m (F); **Torrent Duck** *Merganetta armata*, 22 December 2007 GU 2,750 m (F), female sheltering young chick under wing; **Andean Teal** *Anas andium*, 23 September 2006 PP 3,275 m (F), three chicks following adults, 26 December 2008, MC 4,000 m (F), five recently hatched chicks, 7 February 2009 MC (F); **Carunculated Caracara** *Phalcoboenus carunculatus*, 18 October 2004 MC (I), two eggs, pale red-brown with dark red-brown flecking and sparse white spots, 55.5 × 44.0 mm and 58.6 × 44.9 mm, 6 December 2009, MC (AN, two nests); **Black-chested Buzzard-Eagle** *Geranoaetus melanoleucus*, 1 August 2004, PP 3,900 m (N), 24 May 2009 PP 3,300 m (B) and (N); **Variable Hawk** *Buteo polyosoma*, 23 July 2004 PP 4,100 m (AN); **Black-and-chestnut Eagle** *Oroaetus isidori*, 15 November 2008 GU 2,700 m (B), nest 15 m up in 20-m tree on horizontal branch between bromeliad clumps, adults bringing branches; **Andean Coot** *Fulica ardesiaca*, 17 February 2004 MC (F), adult with four chicks, 17 November 2008 MC (F), three pairs of adults with dependent young, 26 January 2009 YA (F); **Andean Lapwing** *Vanellus resplendens*, 4 December 2007 CO (F), five adults with dependent young, two with two young, three with one, 5 November 2008 MC (F), adult with two young; **Andean Gull** *Larus serranus*, late July 2005 PP 3,275 m (CM), 15 September 2005 PP 3,275 m (AN), on small island in lake, 9 October 2006 PP 3,275 m (F), two fledged young on island in lake, 17 January 2008 PP 3,400 m (N), two older nestlings near fledging on island in lake; **Rock Pigeon** *Columba livia*, 16 June 2005 CO 3,000 m (I), clutch two, in urban area; **Eared Dove** *Zenaida auriculata*, 17 December 2003 QU (B), 3 m up, only one adult building, 19 January 2004 QU (N), 30 January 2004 QU (B), 10 m up, 28 March 2005 QU (B), 3 m up, 31 May 2005 QU 2,900 m (I) clutch two, 15 June 2005 QU 2,850 m (I) clutch two, 11 January 2007 QU (N), 9 December 2008 QU 2,850 m (AN), 5 February 2009 QU (N), 8 August 2009 QU (N), adult carried eggshell and dropped it 30 m from nest; **Black-winged Ground Dove** *Metriopelia melanoptera*, 18 February 2007 MC 3,960 m (I), two all-white eggs, 28.1 × 20.5 mm and 26.7 × 20.7 mm; **Barn Owl** *Tyto alba*, 16 June 2005, CO 3,000 m (F), recently fledged young, 15 February 2007 MC 3,960 m (F); **Band-winged Nightjar** *Caprimulgus longirostris*, 7 October 2008 YA 3,400 m (F); **Sparkling Violetear** *Colibri coruscans*, 14 June 2004 QU 2,700 m

(I), two eggs, both hatched, one nestling eaten by Great Thrush *Turdus fuscater*, 30 May 2005 QU 2,850 m (N), 30 December 2006 PP 3,300 m (B), 1 January 2007 PP central valley slope 3,300 m (I), 27 December 2009 QU near Cumbaya 2,300 m (I), clutch two; **Ecuadorian Hillstar** *Oreotrochilus chimborazo*, 13 September 2004 PP 4,050 m (I), 22 September 2004 PP 4,050 m (B and I), 17 October 2004 PP 4,000 m (I), 5 December 2004 PP 4,050 m (N), 24 September 2005 PP 4,000 m (B), 26 September 2005 PP 4,000 m (B, two nests), 14 October 2006 PP 4,000 m (B), 1 November 2006 PP 4,050 m (I, two nests) and 3,900 m (N), 10 November 2006 PP 3,950 m (B), 18 February 2007 MC 3,960 m (I), 26 October 2007 PP 4,000 m (N), 17 November 2008 MC 3,960 m (B, two nests) and (I), (N) and (AN), 26 December 2008 MC 4,000 m (N, four nests), 2 November 2009 PP 3,850 m (B), 6 December 2009 MC 3,900 m (B) and (I, three nests) and (N, two nests); **Giant Hummingbird** *Patagonia gigas*, 23 October 2008 PP 4,000 m (CM); **Shining Sunbeam** *Aglaeactis cupripennis*, 23 May 2009 PP 3,300 m (B); **Mountain Velvetbreast** *Lafresnaya lafresnayi*, 22 October 2006 PP 3,350 m (I), two fresh eggs, nest 2 m up; **Great Sapphirewing** *Pterophanes cyanopterus*, YA 3,500 m (AN); **Buff-winged Starfrontlet** *Coeligena lutetiae*, 19 December 2006 YA 3,400 m (AN); **Glowing Puffleg** *Eroscnemis vestitus*, 5 November 2006 PP 3,300 m (I), clutch two; **Purple-backed Thornbill** *Ramphomicron microrhynchum*, 12 October 2008 PP 3,800 m (N); **Viridian Metaltail** *Metallura williami*, 11 October 2006 PP 3,300 m (I), 22 October 2006 PP 3,300 m (I), 6 November 2006 PP 3,300 m (N); **Tyrian Metaltail** *M. tyrianthina*, 31 October 2006 PP 3,800 m (B), 2 November 2006 PP 3,300 m (B), 6 November 2006 PP 3,800 m (N), two nestlings; **Rainbow-bearded Thornbill** *Chalcostigma herrani*, 21 December 2006 YA 3,400 m (F), young bird foraging alone, 27 April 2009 YA 3,550 m (CM); **Blue-mantled Thornbill** *Chalcostigma stanleyi*, 23 July 2004 PP 4,100 m (B), 4 August 2004 PP 4,000 m (B) and (I), 11 August 2004 PP 4,000 m (N), 13 September 2004 PP 3,900 m (I), 16 September 2004 PP 3,900 m (I) and 4,050 m (N), 22 September 2004 PP 4,250 m (F), 22 August 2005 PP 4,000 m (I), 27 August 2005 PP 3,900 m (N, two nests), 26 September 2005 PP 4,000 m (N), 11 October 2006 PP 4,000 m (I), and 1 November 2006 PP 4,000 m (I); **Grey-breasted Mountain Toucan** *Andigena hypoglauca*, GU 2,750 m (F); **Bar-bellied Woodpecker** *Veniliornis nigriceps*, 19 November 2006 PP 3,300 m (I), adult entering cavity and remaining for long periods; **White-browed Spinetail** *Hellmayrea gularis*, 22 October 2006 PP 3,340 m (B), this nest described in detail by Greeney & Zyskowski (2008), 7 February 2009 YA 3,500 m (N), two nestlings; **Tawny Antpitta** *Grallaria quitensis*, 7 December 2003 YA 3,400 m (CM), 16 September 2004 PP 4,100 m (I), two eggs, 17 October 2004 PP 4,200 m (N), 22 October 2004 PP 4,150 m (N), 26 September 2005 PP 4,100 m (I, two nests), 28 September 2005 PP 4,250 (B, two nests), 7 October 2005 PP 4,200 m (N), 29 August 2006 PP 4,000 m (B), 27 October 2006 PP 4,000 m (I), 2 February 2009 YA 3,500 m (I) two eggs, and 3,600 m (N, two nests), one nest with two older nestlings, one with two younger nestlings, 5 January 2010 YA 3,500 m (N), two young nestlings; **Ash-coloured Tapaculo** *Myioruis senilis*, 26 January 2009 YA 3,400 m (F); **Blackish Tapaculo** *Scytalopus latrans*, 26 December 2006 YA 3,400 m (F); **White-crested Elaenia** *Elaenia albiceps*, 16 June 2005 CO 3,000 m (B); **Tufted Tit-Tyrant** *Anairetes parulus*, 10 December 2006 PP 3,300 m (N), 26 April 2009 QU 2,900 m (B); **Cinnamon Flycatcher** *Pyrrhomyias cinnamomea* 2 November 2008 GU 2,700 m (B and F), 14 November 2008 GU 2,750 m (F); **Black Phoebe** *Sayornis nigricans*, 30 September 2003 GU 2,700 m (B); **Rufous-breasted Chat-Tyrant** *Ochthoeca rufipectoralis* 20 November 2006 GU 2,750 m (AN); **Black-billed Shrike-Tyrant** *Agrioruis montana*, 27 December 2007 MC 3,960 m (CF), 6 December 2009, MC 3,700 m (N), one addled egg and one older nestling; **Barred Becard** *Pachyramphus versicolor*, 2 November 2008 GU 2,700 m (B); **Red-crested Cotinga** *Ampelion rubrocristatus*, 23 May 2009 PP 3,350 m (N); **Turquoise Jay** *Cyanolyca turcosa*, 20 July 2008 GU 2,750 m (F); **Great Thrush** *Turdus fuscater*, 27 November 2003 QU (N), 17 December 2003 QU (F), 23 September 2004 QU (B), 5 m up, using living sticks with leaves on them, 21 October 2004 PP

3,300 m (I), clutch one, 23 January 2005 PP 3,300 m (B), 10 February 2005 GU 2,750 m (N), 21 September 2006 PP 3,300 m (N), 10 October 2006 PP (B), 12 October 2006 PP 3,300 m (N) fledged two young, 14 October 2006 PP 3,300 m (N), fledged two young, 19 October 2006 PP 3,300 m (AN), destroyed by predator, 20 October 2006 PP 3,300 m (F) male feeding fledgling, 23 October 2006 PP 3,300 m (B), clutch two, 25 October 2006 PP 3,300 m (B), 26 October 2006 PP 3,800 m (B), bringing dry grass to nest, 9 November 2006 PP 3,300 m (B), lining nest with fine grass, 11 November 2006 PP 3,300 m (N), 11 January 2007 QU (CM), 7 May 2009 PP 3,300 m (AN), 23 May 2009 PP 3,350 m (N); **White-capped Dipper** *Cinclus leucocephalus*, 25 December 2009 GU 2,750 m (F); **Brown-bellied Swallow** *Notiochelidon murina*, 15 January 2006 PP 3,300 m (N), three nestlings, 22 September 2006 PP 3,300 m (B), fledged, laid first egg on 23 September, 23 September 2006 PP 4,000 m (CM) and (AN, six nests), adults entering and exiting holes in banks, 29 September 2006 PP 4,000 m (B, four nests), 10 October 2006 PP 3,325 m (I), clutch three, 25 October 2006 PP 4,000 m (B) and (I), fresh all-white egg, 19.9 × 12.7 mm, 27 October 2006 PP 3,800 m (I), two well-developed eggs, 5 November 2006 PP 2,700 m (N), two nestlings, 8 November 2006 PP 3,300 m (N), two nestlings, pin-feathers broken sheaths *c.*¾, 10 November 2006 PP 4,150 m (N), 13 November 2006 PP 3,300 m (N), 14 November 2006 PP 3,300 m (N), three nestlings, pin feathers broken sheaths *c.*¾, 18 November 2006 PP 3,300 m (N) and (F), three fledglings sitting near nest, 12 October 2009 GU 2,700 m (N), in eaves of house; 13 December 2009 PP 4,000 m (AN); **Blue-and-white Swallow** *Notiochelidon cyanoleuca*, all 2 August 2006 OT, three pairs (F), two nests with older nestlings (N); **Rufous Wren** *Cinnycerthia unirufa*, 31 January 2004 GU 2,800 m (N), 3 m up; **Grass Wren** *Cistothorus platensis*, 12 October 2006 PP 3,300 m (B), 18 October 2006 PP 4,050 m (F), 23 December 2006 PP 3,950 m (N); **Mountain Wren** *Troglodytes solstitialis*, 22 September 2006 PP 3,300 m (B), 12 October 2006 PP 3,300 m (N), 14 November 2008 GU 2,750 m (CM); **Páramo Pipit** *Anthus bogotensis*, MC 3,960 m (CF); **Spectacled Whitestart** *Myioborus melanocephalus*, 8 October 2006 PP 3,800 m (B), lining nest, 25 October 2006 PP 3,300 m (B), 26 October 2006 PP 3,800 m (N), two nestlings with pin feathers broken sheaths 1 cm, 27 October 2006 PP 3,800 m (N), two nestlings near to fledging, 17 November 2006 PP 3,300 m (B), 19 November 2006 PP 3,300 m (N), two older nestlings, 12 December 2006 PP 3,300 m (B), lining nest, 13 December 2006 PP 3,300 m (F), 14 December 2006 PP 3,300 m (F), two older fledglings, 2 January 2007 PP 3,375 m (N), two nestlings with pin feathers not broken sheaths, 18 January 2007 PP 3,600 m (F), 17 December 2007 GU 2,800 m (F), 19 October 2008 YA 3,400 m (F), 2 November 2008 GU 2,700 m (F); **Black-crested Warbler** *Basileuterus nigrocristatus*, 9 October 2006 PP 3,275 m (B), clutch two, first laid 18 October, 16 October 2006 PP 3,275 m (N) nest on ground in *Chusquea* sp. bamboo, two nestlings, 13 December 2006 PP 3,300 m (F) pair with older fledgling foraging on own but still being fed, second pair with very young fledglings; **Cinereous Conebill** *Conirostrum cinereum*, 13 October 2006 PP 3,275 m (N), two unfeathered nestlings, 14 October 2006 PP 3,300 m (B), 25 October 2006 PP 3,300 m (CF), 18 January 2007 PP 3,600 m (F); **Blue-backed Conebill** *Conirostrum sitticolor*, 19 October 2008 YA 3,400 m (F); **Masked Flowerpiercer** *Diglossopis cyanea*, 19 November 2006 PP 3,300 m (I), clutch two, 17 December 2007 GU 2,750 m (F), 20 July 2008 GU 2,750 m (F), two young visiting hummingbird feeders, 19 October 2008 YA 3,400 m (F); **Glossy Flowerpiercer** *Diglossa lafresnayii*, 21 July 2008 GU 2,750 m (F), foraging on its own; **Black Flowerpiercer** *D. humeralis*, 21 October 2006 PP 3,350 m (N) nest 2.5 m up in branch tangle, 25 October 2006 PP 3,300 m (B), 2 November 2006 PP 3,300 m (B); **Scrub Tanager** *Tangara vitriolina*, 22 November 2008 QU 2,850 m (B) adult carrying lichens, nest 9 m above ground; **Hooded Mountain Tanager** *Buthraupis montana*, 26 October 2006 Verdecocha, Pichincha 3,320 m (F); **Black-chested Mountain Tanager** *B. eximia*, 1 January 2007 PP 3,300 m (F); **Buff-breasted Mountain Tanager** *Dubusia taeniata*, 14 November 2008 PP 3,400 m (CF); **Black-capped Hemispingus** *Hemispingus*

atropileus, 31 March 2008 GU 2,750 m (F); **Superciliaried Hemispingus** *H. superciliaris*, 16 October 2006 PP 3,300 m (B), 1 January 2007 PP 3,300 m (F), 18 January 2007 PP 3,600 m (F), 28 November 2007 YA 3,400 m (F); **Plushcap** *Catamblyrynchus diadema*, 20 November 2008 GU 2,750 m (F); **Plain-coloured Seedeater** *Catamenia inornata*, 8 February 2004 below YA 2,800 m (B); 14 October 2006 PP 3,175 m (I) clutch two, 16 October 2006 PP 3,300 m (B), 17 October 2006 PP 3,300 m (F), 27 October 2006 PP 3,300 m (N), two nestlings fledged upon approach; **Pale-naped Brush Finch** *Atlapetes pallidinucha*, 18 October 2006 PP 3,300 m (F), 25 October 2006 PP 3,900 m (I), 21 October 2008 GU 2,700 m (B), 14 November 2008 PP 3,400 m (B); **Slaty Brush Finch** *A. schistaceus*, 25 December 2009 GU 2,750 m (F); **Rufous-collared Sparrow** *Zonotrichia capensis*, 27 June 2004 QU (CM), 11 January 2007 QU (N), 8 December 2009 QU 2,900 m (B) and PP 3,300 m (B); **Northern Mountain Cacique** *Cacicus leucoramphus*, 21 July 2008 GU 2,750 m (F); **Hooded Siskin** *Carduelis magellanica*, 15 December 2006 PP 3,300 m (F) female with two older fledglings, 22 February 2008 Yaguarcocha, Imbabura (B).

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Molecular and morphological analysis of Pacific reed warbler specimens of dubious origin, including *Acrocephalus luscinius astrolabii*

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Summary.—Old museum specimens of Pacific reed warblers with dubious origins were sampled genetically. We studied two specimens described as a subspecies of Nightingale Reed Warbler *Acrocephalus luscinius astrolabii*, the origin of which has been tentatively attributed to Micronesia. However, phylogenetic analysis revealed that these specimens are closely related to Tuamotu Reed Warbler *A. atyphus*. We combined these results with morphological characters and a re-evaluation of label data, on the basis of which we suggest that these birds represent an extinct taxon from the Gambier Islands. Other specimens of dubious origin probably came either from the Society or from the Marquesas Islands.

Reed warblers (genus *Acrocephalus*) are widespread in the Pacific, from Micronesia and Australia east to Hawaii and Eastern Polynesia, although several of these insular populations or taxa have reportedly become extinct since the 19th century. Extinctions have been recorded in at least five archipelagos: Mariana (Guam, Pagan), Kiribati (= Line Islands, Fanning), Hawaii (Laysan), Society (Leeward Islands and Mo'orea) and Tuamotu (several atolls) (Holyoak & Thibault 1984, Pratt *et al.* 1987, Fleischer *et al.* 2007, Cibois *et al.* 2008). In the Gambier Islands (Fig. 1), the presence of reed warblers was documented by

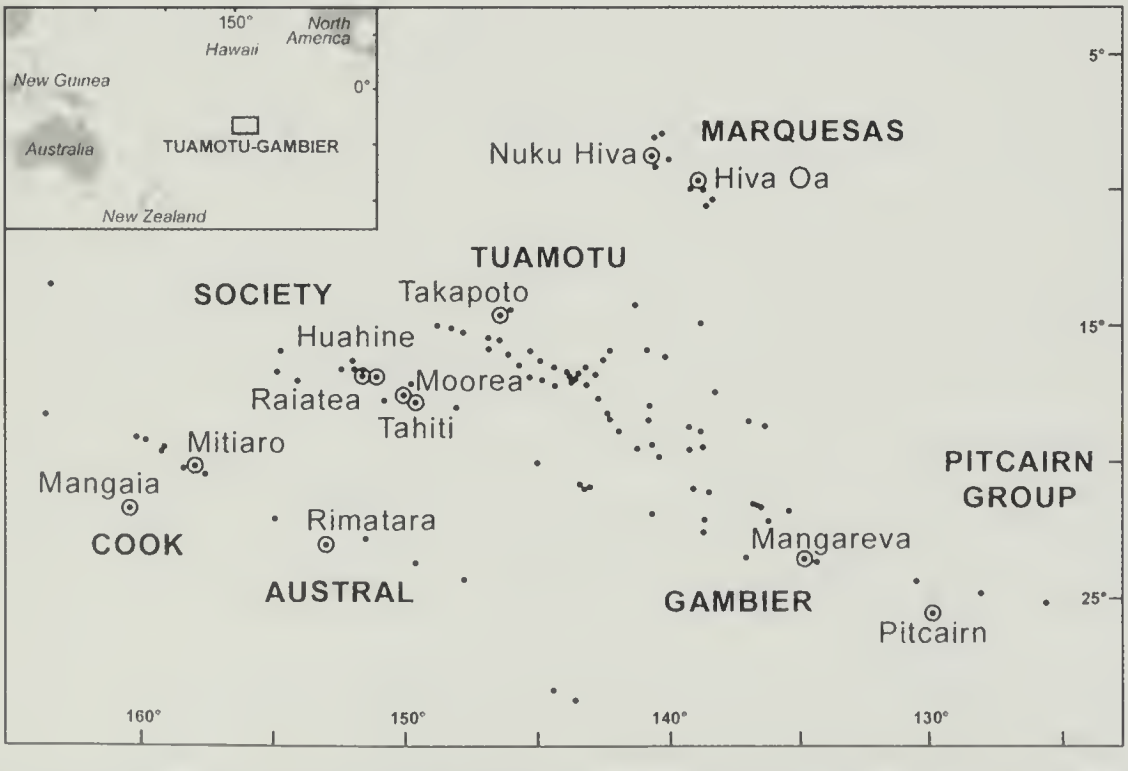

Figure 1. Map of Eastern Polynesia showing islands mentioned both in the text and in Fig. 2. Encircled dots indicate species treated in the phylogenetic tree, except for Nihoa (Hawaii), Kiribati (Line Islands) and Australia, which are not figured.

European navigators during the 19th century (see Discussion) and two specimens held at the Muséum National d'Histoire Naturelle (MNHN, Paris) were suspected to come from there, although their origin was disputed (Holyoak & Thibault 1978). As part of efforts to construct a comprehensive phylogeny of Pacific reed warblers, these specimens were sampled genetically, as were four others of unknown origin from MNHN and the Natural History Museum (BMNH, Tring). Here we present the genetic results for these specimens of dubious origins, compare them to the label information and to their morphological features, and finally discuss their putative identification at species level.

Material and methods

The specimens sampled are described in Table 1. Museum samples were washed with sterile water before extraction, and total genomic DNA was extracted from small pieces (0.5–1.0 cm^2) of skin using a commercial kit (DNeasy Tissue Kit; Qiagen, Valencia, CA, USA). Standard extraction protocols were followed except that the time of proteinase digestion was increased from two to 12 hours, with an additional volume (20 µl) of proteinase K. All tubes and reagents were UV-treated for 30 minutes before use and extraction tubes containing no sample were used as a control for contamination. DNA extracted from museum specimens was degraded, so fragment sizes for amplification were small (*c.*200 bp). Specific primers designed for Pacific reed warblers are given in Cibois *et al.* (2007): sections of both genes were amplified using overlapping fragments. PCR amplifications were performed in 25µl reactions with 2 µl of template and 0.4 µM final concentration for primers. The thermocycling procedure started with an initial denaturation of three minutes at 95°C, followed by 40 cycles of 30 seconds at 95°C, 40 seconds at annealing temperature (50°C), and 40 seconds at 72°C for elongation. PCR products were purified using a Qiagen purification kit and sequenced directly (ABI Prism 377 automated DNA Sequencer) using the same primers. Contiguous sequences derived from the set of sequence fragments were created using Sequencher (Genecodes, Ann Arbor, MI, USA). Sequences were aligned to Pacific and continental reed warbler sequences available in GenBank (Leisler *et al.* 1997, Helbig & Seibold 1999, Cibois *et al.* 2007, Fleischer *et al.* 2007, Cibois *et al.* 2008). The data were subjected to Bayesian inference using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003), with models selected using MrModeltest 2.3 and the AIC criterion (Nylander 2004). We ran two independent runs of four Markov chains for one million generations each. Markov chains were sampled every 100 generations, with a 10% burn-in period.

In the light of the genetic results, we compared the six individuals of dubious origin to reed warblers specimens held in the American Museum of Natural History (AMNH, New York) and the Übersee-Museum Bremen (UMB) collections for the following measurements: wing length (the distance between the carpal joint and tip of the flattened wing), bill length from tip to skull, bill length from tip to rear of nostril, bill width (at rear of nostril), tarsus length (from notch of inter-tarsal joint to lower edge of last complete scale), hindclaw length (chord from tip of claw to edge of the skin of nail), and tail length (from insertion of central pair of feathers to tip of longest rectrix). All measurements were made by AC.

Results and Discussion

Partial cytochrome-*b* gene sequences of 879 bp were obtained for MNHN 1982-769 and MNHN 1847-23. Shorter sequences were obtained for MNHN 1982-768 (412 bp), BMNH 1855.12.19.85 and BMNH 1846.7.29.6 (419 bp). Amplifications were unsuccessful for BMNH 1846.7.29.5. New sequences were deposited in GenBank under accession numbers HQ851084–851087. The alignment was straightforward with no indel, as expected for

TABLE 1

Data on the specimens studied (in bold). MNHN = Muséum National d'Histoire Naturelle, Paris. BMNH = Natural History Museum, Tring. Additional measurements (mean ± standard deviation) are given for four other taxa based on specimens examined in the American Museum of Natural History (AMNH) and the Übersee-Museum Bremen (UMB) collections. All measurements are in mm.

Specimen number	Label data	Wing length	Bill length from tip to skull	Bill length from tip to rear of the nostril	Bill width	Tarsus length	Hindclaw length	Tail length	Putative origin
MNHN 1982-768	Philedon chanteur, Astrolabe[1] Mangareva (*Acrocephalus luscinius astrolabii*)	95	37.2	23.2	5.5	32.5	10.0	95	Gambier
MNHN 1982-769	Philedon, Astrolabe[1] Nouheva (*Acrocephalus luscinius astrolabii*)	99	36.9	22.1	5.4	33.2	10.1	94	Gambier
MNHN 1847.23	(*Acrocephalus caffer*) Tongatabu	91	29	16.9	4.4	27.5	7.8	82	Society Islands
BMNH 1846.7.29.5	Tatare otaitensis, Society Islands, coll. Turner	95†	31.7	18.3	5.2	28.7	9.8	92†	Marquesas or Tahiti
BMNH 1846.7.29.6	Tatare otaitensis, Society Islands, coll. Turner	101	36.9	21.4	5.7	31.8	10.6	88	Leeward Islands (Society Islands)
BMNH 1855.12.19.85	Tatare otaitensis, Society Islands, coll. Zool. Soc.	100	30.6	17.1	5.0	31.2	-	90	North Marquesas
AMNH (*n*=16)	*Acrocephalus caffer* Tahiti (Society Islands)	96.8 ± 2.5	34.3 ± 0.9	19.9 ± 0.8	5.2 ± 0.2	32 ± 1	9.0 ± 0.3	91.2 ± 5.0	
AMNH (*n*=15)	*Acrocephalus percernis* Nuku Hiva (North Marquesas)	98.4 ± 3	29.2 ± 1.1	17.6 ± 0.4	5.1 ± 0.2	32 ± 1	9.7 ± 0.4	95.5 ± 8.0	
AMNH 594897	*Acrocephalus musae garretti* Huahine (Leeward Islands, Society Islands)	103	36.8	21.7	5.3	33.2	10.5	103†	
UMB 7947	*Acrocephalus m. musae* Raiatea (Leeward Islands, Society Islands)	101	37.5	21.7	5.4	32.0	10.0	92	
AMNH 190398	*Acrocephalus longirostris* Mo'orea (Society Islands)	104	37.8	22.4	5.3	30.8	9.9	98	
AMNH (*n*=15)	*Acrocephalus atyphus* Fa'aite (Tuamotu)	89.5 ± 2.4	26.5 ± 1.3	15 ± 0.6	4.7 ± 0.4	30.1 ± 0.6	8.3 ± 0.3	90 ± 4	

[1] *Astrolabe* was one of the ships used by Dumont d'Urville's expedition in the Pacific Ocean (1838–39)
† Incomplete length due to feather wear

a protein-coding gene. We translated the nucleotide sequences to proteins using Mega (Tamura *et al.* 2007) and found no stop codon. We detected no contamination in the negative controls. The sequences of MNHN 1982-768 and 1982-769 were identical. The sequence of BMNH 1855.12.19.85 was identical to that of Northern Marquesan Reed Warbler *A. percernis*. The sequence of BMNH 1846.7.29.6 differed by one transversion from the sequence of the Leeward Islands Reed Warbler *A. musae garretti* from Huahine. The sequence of MNHN 1847-23 differed by seven bases (five transitions and two transversions) from Tahiti Reed Warbler *A. caffer*. Uncorrected pair-wise distances are given in Table 2.

Results from the AIC criterion in MrModeltest supported the GTR + I + G model (General Time Reversible + Proportion Invariant + Gamma: Lanave *et al.* 1984, Rodriguez *et al.* 1990) for the dataset. The phylogenetic tree obtained using MrBayes is presented in Fig. 2. Results for the main Polynesian lineages were detailed in previous works so we only focused on the placement of specimens of dubious origin. The two *astrolabii* (MNHN 1982-768 and 1982-769) formed a well-supported clade with *A. percernis* and Tuamotu Reed Warbler *A. atyphus* (0.99 Bayesian posterior probabilities PB). Within this group, *atyphus* and *astrolabii* were sister taxa but with low support (0.74 PB). MNHN 1847-23 was sister taxon to *caffer* with good support (1 PB). BMNH 1855.12.19.85 branched off with *percernis* (same haplotype, 0.97 PB due to the shorter sequence), whereas BMNH 1846.7.29.6 was sister to *musae* (Huahine and Raiatea, Society Islands) with good support (1.0 PB).

MNHN 1982-768 and 1982-769: Acrocephalus luscinius astrolabii.—The labels of these two specimens bear similar handwriting, indicating 'Mangareva, Astrolabe, Philedon chanteur', numbered 151 and registered as number E 8681 in the *Catalogue des Oiseaux* no. 3 of the MNHN ornithological collection for MNHN 1982-768, and 'Philedon, Nouheva [or Nouhiva], Astrolabe' numbered 266, with no registration number, for MNHN 1982-769. In accordance with the label of the first specimen, Lacan & Mougin (1974) suggested that both originated from the island of Mangareva in the Gambier archipelago. However, Holyoak & Thibault (1978) rejected this hypothesis based on the lack of agreement between the labels (Nouheva / Nouhiva, an unknown locality that could be an approximation of Nuku Hiva in the Marquesas) and the similarity in coloration and biometry of the specimens to Nightingale Reed Warbler *A. luscinius* of Micronesia. They proposed a new subspecies, *A. luscinius astrolabii* (type specimen MNHN 1982-768), from an unknown island of Micronesia, tentatively attributed to Yap. Holyoak & Thibault (1978) were influenced by (a) their coloration being very similar to forms of *A. luscinius*, and (b) that the type was registered in the MNHN catalogue as E 8681 following 'D 8681 *Acrocephalus* syrinx K et F. Carolines-Hombron et Jacquinot 1841-106' from Micronesia.

Molecular data suggest that the two *A. l. astrolabii* specimens have the same origin: both possess a unique cytochrome-*b* haplotype and they are more closely related to Northern Marquesan and Tuamotu Reed Warblers than to any other Pacific reed warblers studied, particularly to *A. luscinius* (Fig. 2). The Tuamotu archipelago is the closest group of islands to the Gambier archipelago (Fig. 1). Morphologically the two specimens are distinct from *A. percernis* and *A. atyphus* (Fig. 3), with on average a bill longer than *percernis* and *atyphus*, a wing longer than *atyphus* but similar to *percernis* (Table 2), and brown plumage which recalls more that of *atyphus* than the yellow coloration of Marquesas reed warblers (Pratt *et al.* 1987). Because the labels of both *A. l. astrolabii* specimens mention 'Astrolabe' and both possess a unique haplotype closely related to Tuamotu Reed Warbler, it is probable that they were collected in the Gambier Islands during the Antarctic Expedition commanded by Captain J. S. C. Dumont d'Urville aboard the two ships *Astrolabe* and *Zélée*, with the naturalists J.-B. Hombron and H. Jacquinot. This expedition travelled extensively in the

TABLE 2

Pair-wise sequence divergence found in the cytochrome-*b* sequences (% uncorrected values). The five specimens studied are indicated in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. *A. aequinoctialis* EF156278																			
2. MNHN 1982.768	3.3																		
3. MNHN 1982.769	3.3	0.0																	
4. *A. atyphus* EF156281	3.0	0.9	0.9																
5. *A. australis* AJ004305	1.5	3.0	3.0	3.3															
6. *A. caffer* EF156308	2.7	1.2	1.2	1.5	2.4														
7. *A. familiaris kingi* EU119965	3.3	3.6	3.6	3.9	3.0	3.0													
8. *A. musae garretti* EU303306	2.7	2.1	2.1	2.4	3.0	2.1	3.0												
9. *A. m. musae* EU303310	3.6	3.0	3.0	3.3	3.9	3.0	3.9	0.9											
10. *A. kerearako kaoko* EF156291	2.7	3.6	3.6	3.9	3.0	3.0	3.6	3.6	4.5										
11. *A. k. kerearako* EF156292	2.4	2.7	2.7	2.4	2.7	2.1	3.3	2.4	3.0	2.1									
12. *A. longirostris* EU303308	3.3	1.5	1.5	1.8	3.6	2.1	3.6	1.8	2.4	4.2	2.7								
13. *A. mendanae* EF156287	0.3	3.0	3.0	2.7	1.2	2.4	3.0	2.4	3.3	2.4	2.1	3.0							
14. MNHN 1847.23	3.3	1.8	1.8	2.1	3.0	0.6	3.6	2.1	3.0	3.6	2.7	2.7	3.0						
15. BMNH 1846.7.29.6	2.7	1.8	1.8	2.1	3.0	1.8	3.0	0.3	1.2	3.6	2.1	2.1	2.4	1.8					
16. BMNH 1855.12.19.85	3.3	0.6	0.6	1.5	3.0	1.2	3.6	2.1	3.0	3.6	2.7	1.5	3.0	1.8	1.8				
17. *A. percernis* EF156299	3.3	0.6	0.6	1.5	3.0	1.2	3.6	2.1	3.0	3.6	2.7	1.5	3.0	1.8	1.8	0.0			
18. *A. rimitarae* EF156305	2.4	2.1	2.1	2.4	2.1	1.5	3.3	2.4	3.3	2.1	1.2	3.0	2.1	2.1	2.1	2.1	2.1		
19. *A. taiti* AJ004308	4.8	4.5	4.5	5.4	4.5	3.9	5.7	4.8	5.7	5.7	4.8	5.4	4.5	4.5	4.5	4.5	4.5	4.2	
20. *A. luscinius* HQ844366	0.6	3.3	3.3	2.4	1.5	2.1	3.3	2.7	3.6	2.7	2.4	3.3	0.3	2.7	2.7	3.3	3.3	2.4	4.8

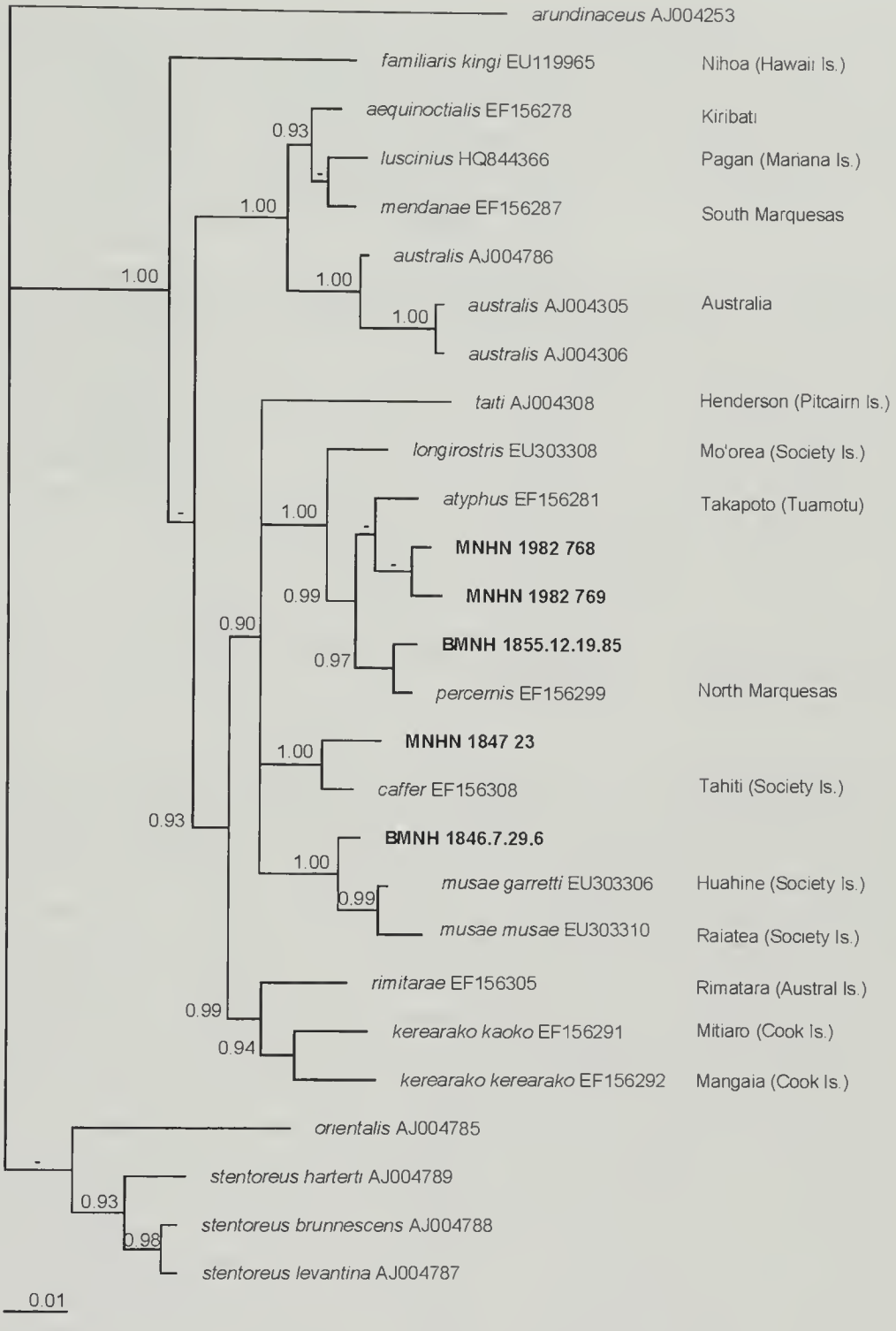

Figure 2. Phylogenetic tree estimated using Bayesian inference and partial cytochrome-*b* sequences. Numbers by nodes refer to posterior probabilities; dashes indicate probabilities inferior to 0.90. GenBank numbers are indicated beside the taxon name, and the specimens of dubious origin are indicated in bold.

tropical Pacific in 1838–39 and visited numerous islands in Polynesia and Melanesia, as well as a few in Micronesia. They reached Mangareva on 3 August 1838 (Dumont d'Urville 1842) and visited the four main islands, Mangareva, Aukena, Taravai and Akamaru. A detailed catalogue of the ornithological collection was never published as explained in Jacquinot & Pucheran (1853) but according to the labels of specimens still present at MNHN, the expedition collected at least these two reed warblers, a Pacific Reef Heron *Egretta sacra* (MNHN 195) and the type specimen of Tuamotu Kingfisher *Halcyon gambieri* (MNHN 2006-555).

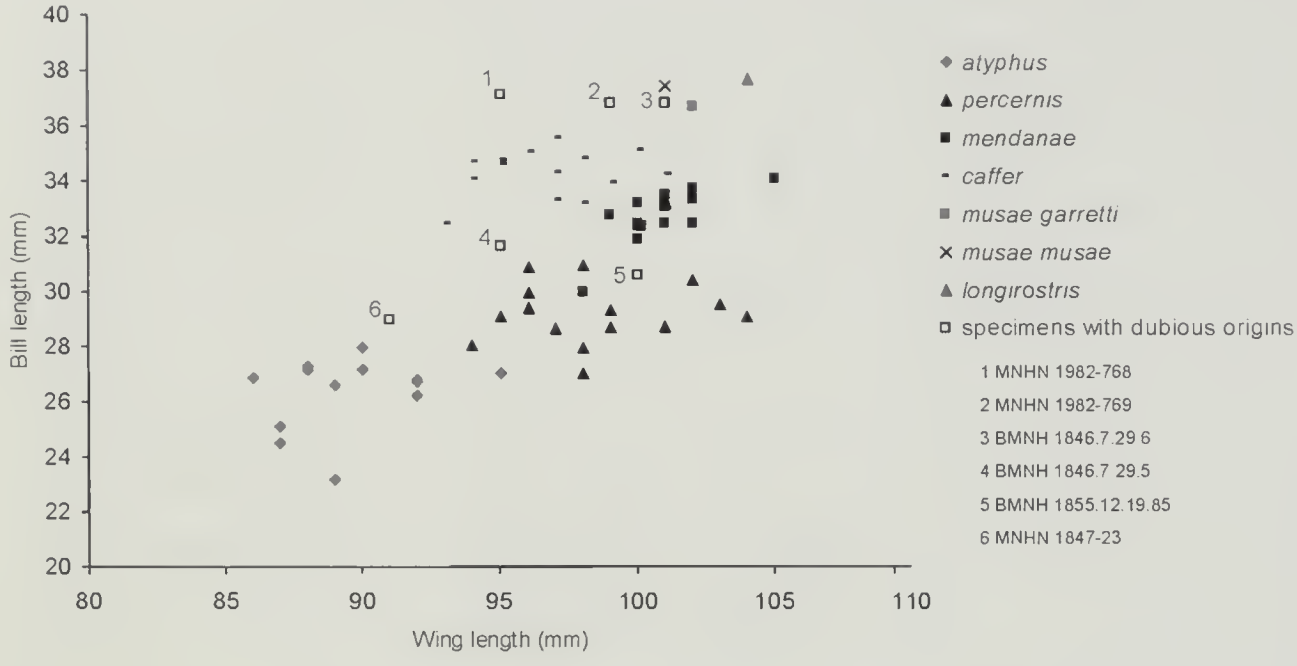

Figure 3. Bill length (from tip to skull) vs. wing length for those specimens of dubious origin and several eastern Polynesian reed warbler taxa (see Table 1).

To our knowledge no other reed warbler specimen from the Gambier Islands exists in ornithological collections. In addition to Dumont d'Urville's expedition, two other expeditions reached the archipelago during the first half of the 19th century and recorded reed warblers. During his expedition to the Bering Strait and the Pacific islands, Frederick William Beechey visited the Gambier Islands for a few days in January 1826. There he observed a bird that corresponds quite well to a reed warbler: 'a species of turdus, somewhat resembling a thrush in plumage, but smaller, possessing a similar though less harmonious note' (Beechey 1832: 123). Two years after Dumont d'Urville's expedition, Pierre-Adolphe Lesson, who served as a surgeon on the *Pylade*, visited Mangareva for nine days in April 1840, where he observed and collected a reed warbler ('Je tuais aussi un oiseau du genre philedon': Lesson 1844: 62). Unfortunately the fate of this specimen, like most of the ornithological collection gathered by the two Lesson brothers, is unknown. Additional evidence suggests that reed warblers were still present on the Gambier Islands during the second part of the 19th century. In their comments on specimens collected by Andrew Garrett in the 1870s for the Godeffroy Museum in Hamburg, Schmeltz & Krause (1881: 238) mentioned that reed warblers were likely found in the Gambiers ('Soll auch auf den Gambier-Inseln vorkommen'), although no specimen was specifically mentioned. Wiglesworth (1891) also included the Gambier Islands in the distribution of *Acrocephalus* (with Garrett as collector), but we do not know whether he had access to a specimen or if he merely based this information on Schmeltz & Krause's comment. In the early 20th century, the birds were never observed again by ornithologists (e.g. the Whitney South Sea Expedition in 1922) or naturalists (e.g. Alvin Seale in April 1902; Seale 1901–02) but two testimonies provide the last evidence of the former presence of reed warblers in the Gambiers. In 1922, the chief of Taravai, one of the islands of the archipelago, described a bird similar to a reed warbler but which had not been seen for 30 or 50 years to Ernst Quayle, the collector of the Whitney South Sea Expedition organised by the American Museum of Natural History (Quayle ms; vol. K, p. 122). During the Mangarevan Expedition organised by the Bernice P. Bishop Museum in 1934, the archaeologist Kenneth Emory noted that the Polynesians of the

Gambiers still used the name 'Komako' for a bird no longer present there (Te Rangi Hiroa 1938): it is the current name for *Acrocephalus* spp. in the Marquesas and some Tuamotu islands (Holyoak & Thibault 1984), and also that mentioned by Lesson (1844) and Tregear (1899). No fossil remains of reed warblers have been obtained from archaeological sites in the Gambiers (Worthy & Tennyson 2004), but bones of small passerines have rarely been found by such surveys on Pacific Islands (Steadman 2006).

Other specimens of dubious origin.—Peale (1848) included Samoa and Tonga (= Tongatabu) as localities for specimens of *Acrocephalus* reed warblers collected during the United States Exploring Expedition in the Pacific Ocean (1838–42). However, Finsch (1872) did not obtain such birds in Samoa and Tonga and doubted that a reed warbler inhabited these islands. Specimen MNHN 1847-23 is labelled 'Tongatabu', but genetically this individual is closely related to Tahiti Reed Warbler. It is obviously smaller than other individuals from Tahiti (Table 1, Fig. 3) but its plumage is typical of pale phase Tahitian birds, being yellow below and olive above with pale feather fringes (Pratt *et al.* 1987). Thus plumage and genetic data suggest that this specimen was probably collected in the Society Islands, maybe Tahiti, but not on Tonga, in accordance with the absence of confirmed information on the past presence of reed warblers in Central Polynesia (Tonga or Samoa). We propose to classify this bird as *A. caffer* (Society Islands).

The three specimens held at BMNH were provisionally all classified as '*Acrocephalus caffer*?', and were all probably collected during the second quarter of the 19th century. They possess bright yellow underparts that correspond to either the Society Islands or the Marquesan birds. BMNH 1855.12.19.85 possesses the same cytochrome-*b* haplotype as Northern Marquesan Reed Warbler: its bill is shorter than birds from the Society Islands and corresponds well to that of *A. percernis* (Fig. 3). We propose to classify this specimen under *A percernis* subsp. (Marquesas Islands), with uncertainty regarding the island and subspecies concerned. The two other specimens were collected by Turner, a dealer who supplied 13 specimens of Pacific island birds in 1846, registered under 1846.7.29.1–13. Neither warbler specimen has an original label, only the museum ones which state 'Society Is.' (Table 1), but the register indicates 'Noukaiva' for these two specimens (R. Prŷs-Jones *in litt.* 2010). The DNA sequence obtained for BMNH 1846.7.29.6 contradicts the register information, as this individual is sister taxon to the Leeward Islands reed warblers (Huahine and Raiatea, Society Islands) with good support in the phylogenetic tree (Fig. 2). Moreover, its measurements are similar to those of the taxon from Huahine *A. musae garretti* (Table 1, Fig. 3). Reed warblers are known only from Huahine and Raiatea (two populations extinct today; Cibois *et al.* 2008) but the former distribution of reed warblers in the Leeward Islands could have included other localities. We propose to classify this bird as *A. musae* subsp. (Leeward Islands), with uncertainty regarding the island and subspecies. Unfortunately no sequence was obtained for BMNH 1846.7.29.5. The bill of this specimen is smaller than that of warblers from Tahiti and could correspond to Marquesan birds (Fig. 3), in accordance with the register information, but uncertainty regarding the provenance of this specimen persists.

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First records of White-winged *Nyctibius leucopterus* and Rufous Potoos *N. bracteatus* in Venezuela

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Summary.—We discuss the first records for Venezuela of White-winged *Nyctibius leucopterus* and Rufous Potoos *N. bracteatus*. These species remained virtually unknown until *c*.20 years ago, yet recent work has found both to be widely distributed in lowland forest from the Guianas south through Amazonian Brazil and west to Peru (with *N. bracteatus* also recorded in Bolivia, Ecuador and Colombia). *N. leucopterus* can be relatively numerous and its habitat preferences may not be as specialised as once thought; however, *N. bracteatus* appears to be scarce and of only local occurrence throughout its range. Despite their widespread occurrence, both species remain poorly known as a result of their nocturnal behaviour and habit of singing only a few nights per month concentrated around the full moon. We use sonograms to illustrate vocal variation and to document unpublished records of both species.

Birds arguably represent the best-known class of vertebrates with respect to biogeographic patterns, yet the distribution and abundance of many species remain poorly known across large parts of the world. Even in the most intensively studied regions, such as North America and Europe, new species are recorded almost annually (e.g., Sharrock & Grant 1982, Hamilton *et al.* 2007). In all but a very few instances, however, records of new species in these regions involve either vagrants of migratory species or precursors of range expansion, the latter often at the margin of the species' range. Most tropical regions, in contrast, remain relatively poorly known biogeographically, so even the core breeding range for some species has yet to be established. Recent discoveries most often involve cryptic species or those that are easily overlooked, and many species remain poorly known as a result of their similarity to other species, low population density, inconspicuous vocalisations, occurrence in areas difficult to survey or in regions or habitats overlooked in the past (such as islands in the Orinoco and Amazon rivers, or isolated mountain ranges), or because their activity or vocal patterns correspond to periods when few workers are in the field (e.g., nocturnal species or those most active during tropical wet seasons) (Cohn-Haft 1993, Zimmer 1997, Isler *et al.* 2001, Zimmer *et al.* 2001, Hilty & Ascanio 2009).

One of the more remarkable discoveries in recent years involved a Neotropical species, White-winged Potoo *Nyctibius leucopterus*. Unrecorded for over 150 years in its previously known range in the Atlantic Forest of eastern Brazil, the species was rediscovered 2,500 km distant in central Amazonia (Cohn-Haft 1993). Equally remarkable is that in the 20 years since *N. leucopterus* was discovered in Amazonia an emerging pattern suggests that the species occurs locally throughout much of the basin, with recent encounters in all three Guianas, Peru and at widely scattered sites across Amazonian Brazil (Cohn-Haft 1993, Parker 1993, Alvarez & Whitney 2003, Claessens *et al.* 2005, Ridgely *et al.* 2005, Ottema *et al.* 2010).

Rufous Potoo *N. bracteatus*, also virtually unknown in life for almost 150 years following its description in the mid-19th century, is likewise poorly known yet distributed widely in Amazonia (Cohn-Haft 1999). Although the species has been recorded from most

Amazonian countries, it is known from relatively few specimens and sightings at widely scattered sites across the region, from the Guianas and central Amazonian Brazil to Ecuador and northern Bolivia (Snyder 1966, Parker *et al.* 1982, 1996, Sick 1993, Cohn-Haft *et al.* 1997, 2007, Ridgely & Greenfield 2001, Cleere & Ingels 2002, Ridgely *et al.* 2005, Restall *et al.* 2006, Ingels *et al.* 2008; S. K. Herzog pers. comm.).

With a long ornithological history, primarily through the collecting efforts of William H. Phelps and his son, William H. Phelps, Jr. (Rodriguez 2006), Venezuela may be the South American country in which avian distributions are best known. With just over 1,350 species recorded in an area not much larger than the state of Texas, Venezuela ranks sixth in number of species among South American countries (Hilty 2003, Remsen *et al.* 2010). Nevertheless, 11 new species have been recorded in Venezuela since the publication of Hilty's (2003) comprehensive guide (Ascanio 2009). Of these, only Eurasian Wigeon *Anas penelope* (Williams & Beadle 2003), Yellow-nosed Albatross *Thalassarche chlororhynchos* (Marín *et al.* 2010) and Black-legged Kittiwake *Rissa tridactyla* (Kirwan *et al.* 2009) are best considered vagrants. Three of the remaining eight species are recently or yet to be described endemics to Venezuela: Carrizal Seedeater *Amaurospiza carrizalensis* (Lentino & Restall 2003), Río Orinoco Spinetail *Synallaxis beverlyae* (Hilty & Ascanio 2009) and an undescribed species of softtail *Thripophaga* sp. nov. (Hilty *et al.* in prep.). The other five species probably breed in the country.

Given the presence of much suitable Amazonian forest in the south and east of the country, and the depth at which the country's avifauna has been studied, it remained somewhat of an anomaly that *N. leucopterus* and *N. bracteatus* were unrecorded in Venezuela (see Cohn-Haft 1999).

Based on sight observations and audio recordings made during our field work in eastern Venezuela, we provide details for the northernmost records of *N. leucopterus*, a record near the northernmost limit of the range for *N. bracteatus*, and the first records of both species from Venezuela. We place these records into a geographical context using published reports of both species and unpublished observations by CAM that extend their known ranges within Amazonian Brazil. We also present sonograms of both species, both to document our records and to illustrate the vocalisations of two species that are poorly sampled vocally.

White-winged Potoo *Nyctibius leucopterus*

During field work within the northern section of the Imataca Forest Reserve, in the state of Delta Amacuro, east of El Palmar and the logging camp at Río Grande, CAM & BED searched for nocturnal birds on several nights during the full-moon cycle in mid-April 2006. Late in the evening on 11 April, we used whistled imitations of the song of *N. leucopterus* to locate a single bird in tall *terra firme* forest 14.1 km from the main road behind the logging camp at Río Grande (08°12'17"N, 61°43'47"W; *c.*275 m). The following night (12 April 2006), we found an apparent pair of *N. leucopterus* along a different logging road 9.6 km beyond the bridge over the río Grande (08°04'54"N, 61°37'58"W; 280 m). Two of these birds were well seen and CAM recorded their vocalisations. In both instances, we heard these birds only after imitating the species' song and, even following imitation, the birds called frequently but they sang only a few times. Both birds we saw perched in or near the forest canopy, often on exposed branches.

After imitating the descending whistle of *N. leucopterus* at each of the many stops we made in the evening on 11 April 2006, CAM heard the species' repeated *wert* or *pwit* calls. The bird subsequently sang six times, of which CAM was able to record three songs (Figs. 1A–B), but it called frequently after the whistled imitations, and many calls were recorded

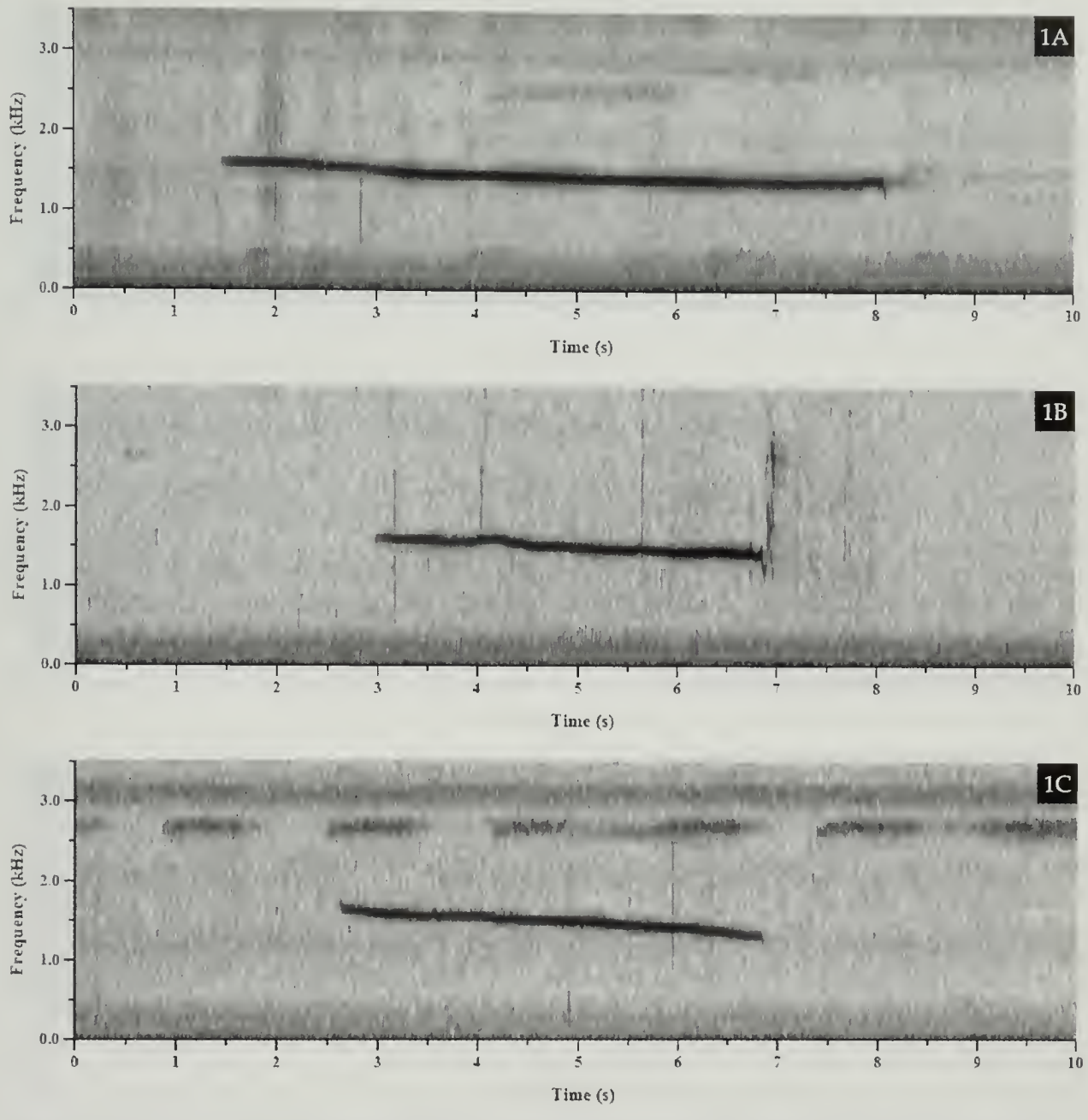

Figure 1A. Typical song by White-winged Potoo *Nyctibius leucopterus* recorded after human imitation is a clear whistle of almost seven seconds in duration that descends in frequency from 1,600 Hz to 1,400 Hz. Sonogram from recording made on 11 April 2006 at Imataca Forest Reserve, Bolívar, Venezuela (CAM field recording file 2006-BOL257). This and all other sonograms made using Raven 1.2.1 (Cornell Lab of Ornithology, Ithaca, New York) using a Hann window setting, a sample and DFT size of 1,024, and an overlap of 90%. The horizontal axis represents time in seconds and the vertical axis is frequency in kHz.

Figure 1B. Agitated song by the same White-winged Potoo *Nyctibius leucopterus* recorded after additional imitation is also a clear and slightly descending whistle of about the same frequency range, but it is shorter in duration (four seconds) and concludes with a conspicuous 'chip'. From recording made on 11 April 2006 at Imataca Forest Reserve, Bolívar, Venezuela (CAM field recording file 2006-BOL258).

Figure 1C. Song by a second White-winged Potoo *Nyctibius leucopterus* recorded after human imitation is likewise a clear but also a more strongly descending whistle (1,650 Hz descending to 1,300 Hz) of *c.*4 seconds duration. From recording made on 12 April 2006 at Imataca Forest Reserve, Bolívar, Venezuela (CAM field recording file 2006-BOL285).

(Fig. 2A). We saw this bird once briefly as it flew overhead, and we twice obtained relatively good views through a 15–45× spotting scope while we spotlighted the bird as it perched at the edge of the canopy of trees along the road. The description below, based on audio notes recorded by CAM shortly after the observation, clearly identifies the bird as *N. leucopterus*

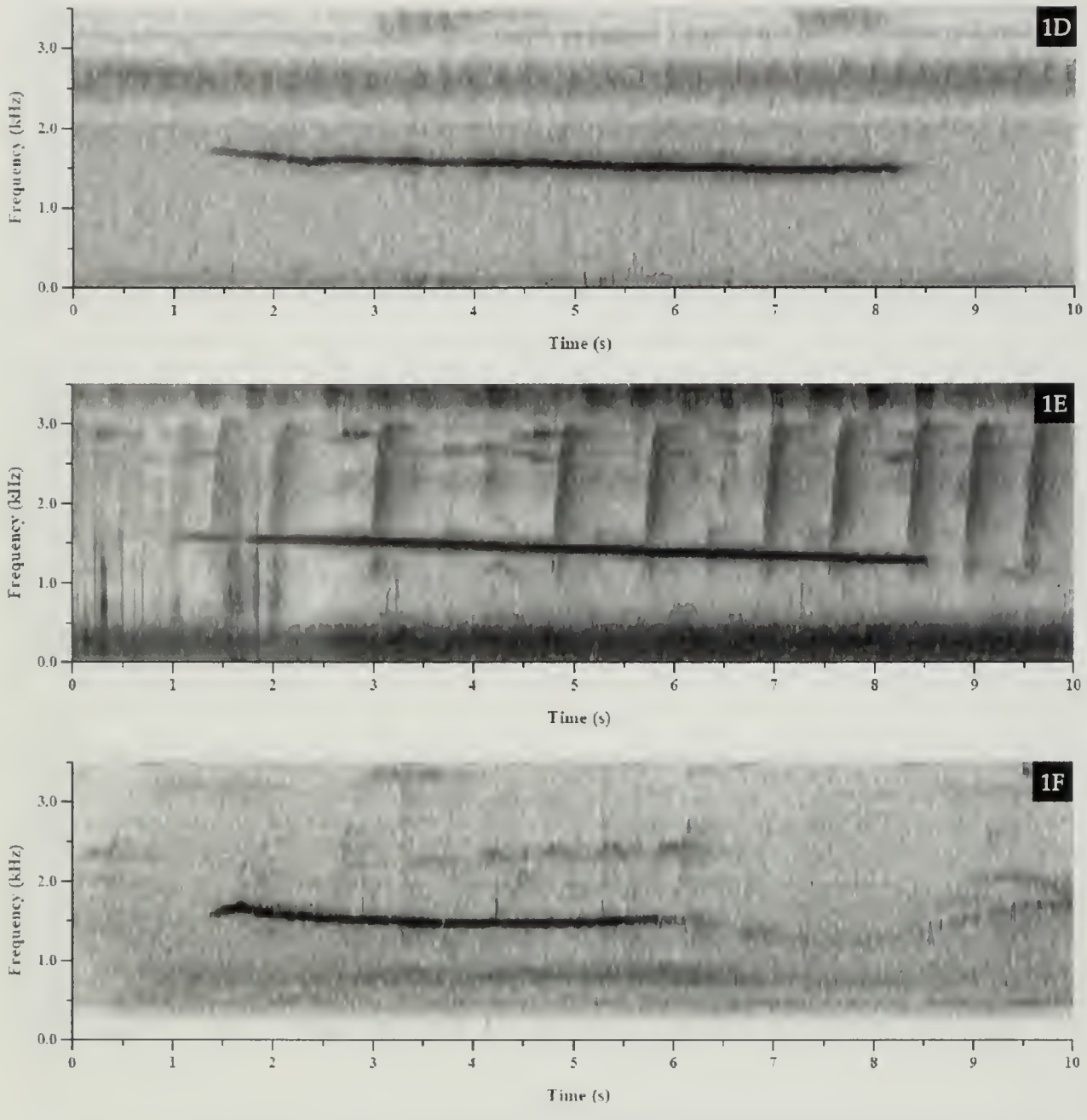

Figure 1D. Song of White-winged Potoo *Nyctibius leucopterus* north of Manaus, Amazonas, Brazil (recording by M. Cohn-Haft taken from Naka *et al.* 2008). This song is about seven seconds in duration and descends from 1,735 Hz to 1,500 Hz, a frequency range slightly higher than that of our Venezuelan recordings.

Figure 1E. Song by White-winged Potoo *Nyctibius leucopterus* after whistled imitation, recorded by CAM just before dawn on 7 December 2000 at Fazenda Toshiba, Município de Careiro do Castanho, Amazonas, Brazil (LNS 127608). This song descends gradually from 1,575 Hz to 1,275 Hz during its 7.5 seconds duration.

Figure 1F. Song of White-winged Potoo *Nyctibius leucopterus* from Floresta Nacional da Caxiuanã, Pará, Brazil, recorded by K. J. Zimmer and taken from Marantz & Zimmer (2006). This song of *c.*4.6 seconds in duration first ascends slightly from 1,570 Hz to 1,670 Hz before descending to *c.*1,500 Hz, a frequency range comparable to that of our Venezuelan recordings.

despite its being subject to the vagaries of field observation under the less than ideal conditions involved with spotlighting a bird in the forest canopy. The bird was about the size of an American Kestrel *Falco sparverius*, but with a proportionately large head, a sloping forehead, a somewhat flat-crowned appearance and what appeared to be a relatively large bill. The plumage was primarily dark, greyish brown, with a mottled appearance and a conspicuous white panel on the wing. This patch, which was relatively large and slightly curved to crescent-shaped, appeared to extend almost throughout the secondary-coverts.

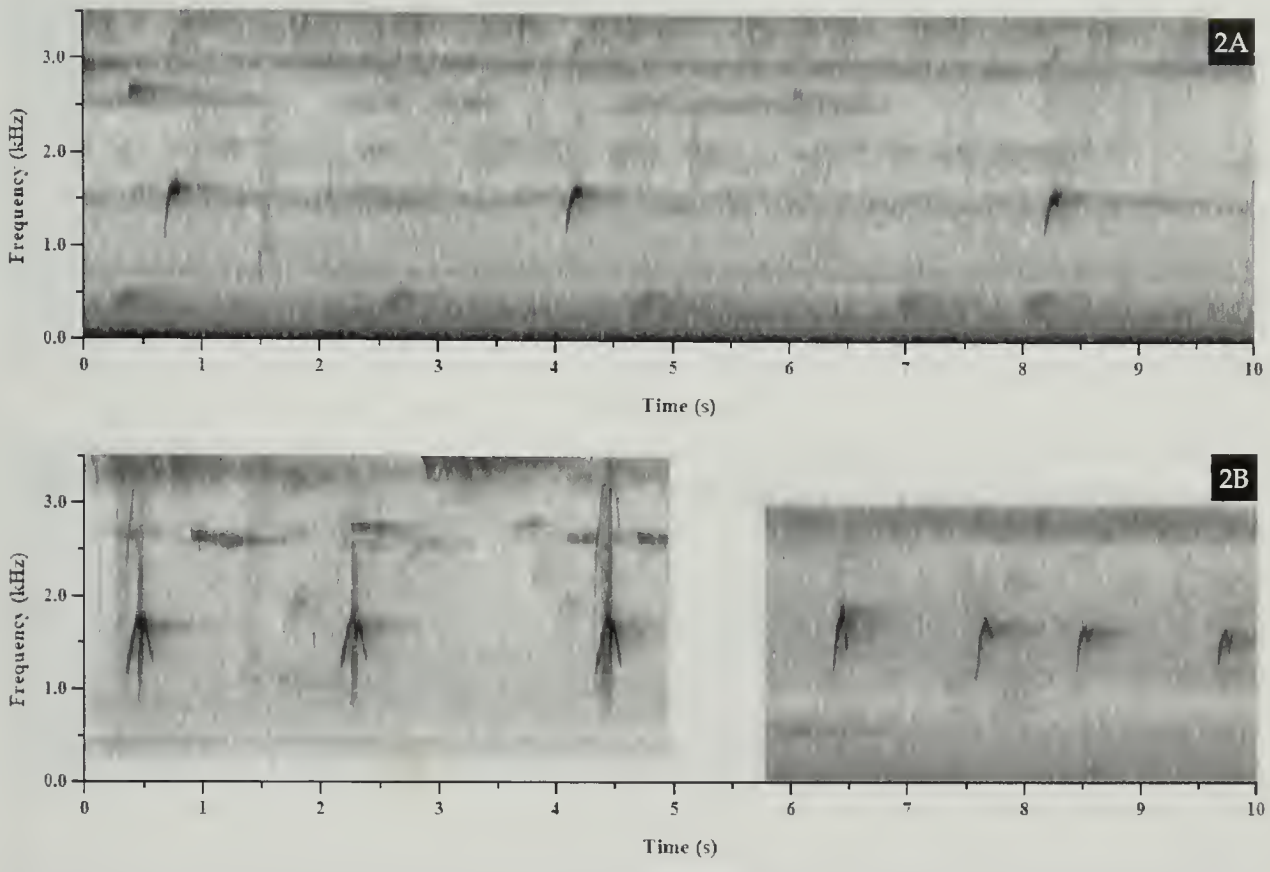

Figure 2A. Three soft *wert* calls by White-winged Potoo *Nyctibius leucopterus* recorded after human imitation of the song. Notes with an inverted 'J' shape ascend from *c*.900 to 1,700 Hz in a period of *c*.0.15 seconds. Note also that the third note in this series has a weak frequency modulation that is typical of calls at least by birds on the south bank of the Amazon River near Manaus (on basis of recordings from Marantz & Zimmer 2006 and Naka *et al*. 2008). The recording was made on 11 April 2006 at Imataca Forest Reserve, Bolívar, Venezuela (CAM field recording file 2006-BOL256).

Figure 2B. Calls by White-winged Potoo *Nyctibius leucopterus* at sites near Manaus, Amazonas, Brazil. The three calls on the left were recorded by CAM on 11 December 2000 *c*.100 km south of the Amazon River at Fazenda Toshiba, Município de Careiro do Castanho, Amazonas, Brazil (LNS 127653, taken from Marantz & Zimmer 2006). The four calls on the right were recorded by M. Cohn-Haft north of Manaus (taken from Naka *et al*. 2008). The calls from Fazenda Toshiba represent notes with an inverted 'W' shape and a small frequency modulation. In contrast, the calls recorded north of Manaus are more like those from Venezuela, with an inverted 'V' shape that lacks the frequency modulation. The frequency range of all three sets of calls is comparable, with an increase from 1,050–1,100 Hz to 1,700–1,900 Hz in a period of 0.12–0.25 seconds, but note also that the frequency range in the latter series of four calls descends slightly. The white region at the bottom of the left sonogram and at the top of the one on the right reflect filtering for the published recordings.

Also evident were fine, dark shaft-streaks extending vertically across the white wing-panel. The tail was about as long as the body, essentially parallel-sided, despite tapering inward slightly near the tip, and brownish grey with some relatively indistinct, dark barring.

The birds we encountered the following evening behaved in a similar manner in that both were silent prior to our imitating their songs, and even after these imitations, they gave primarily the soft *wert* calls; however, one bird did give several songs: a clear, descending whistle of *c*.5–7 seconds in duration (of which five examples were recorded; Fig. 1C). The bird we saw remained high in the canopy, where it perched atop an exposed snag. We did not take a detailed description, but this bird was also a small potoo with a bold, white blaze across the middle part of the wing. A second bird was calling nearby, but we saw only one of the two birds heard this evening. As a result of previous logging, the forest at this site was somewhat scrubbier than that where we found the previous night's bird, but the canopy

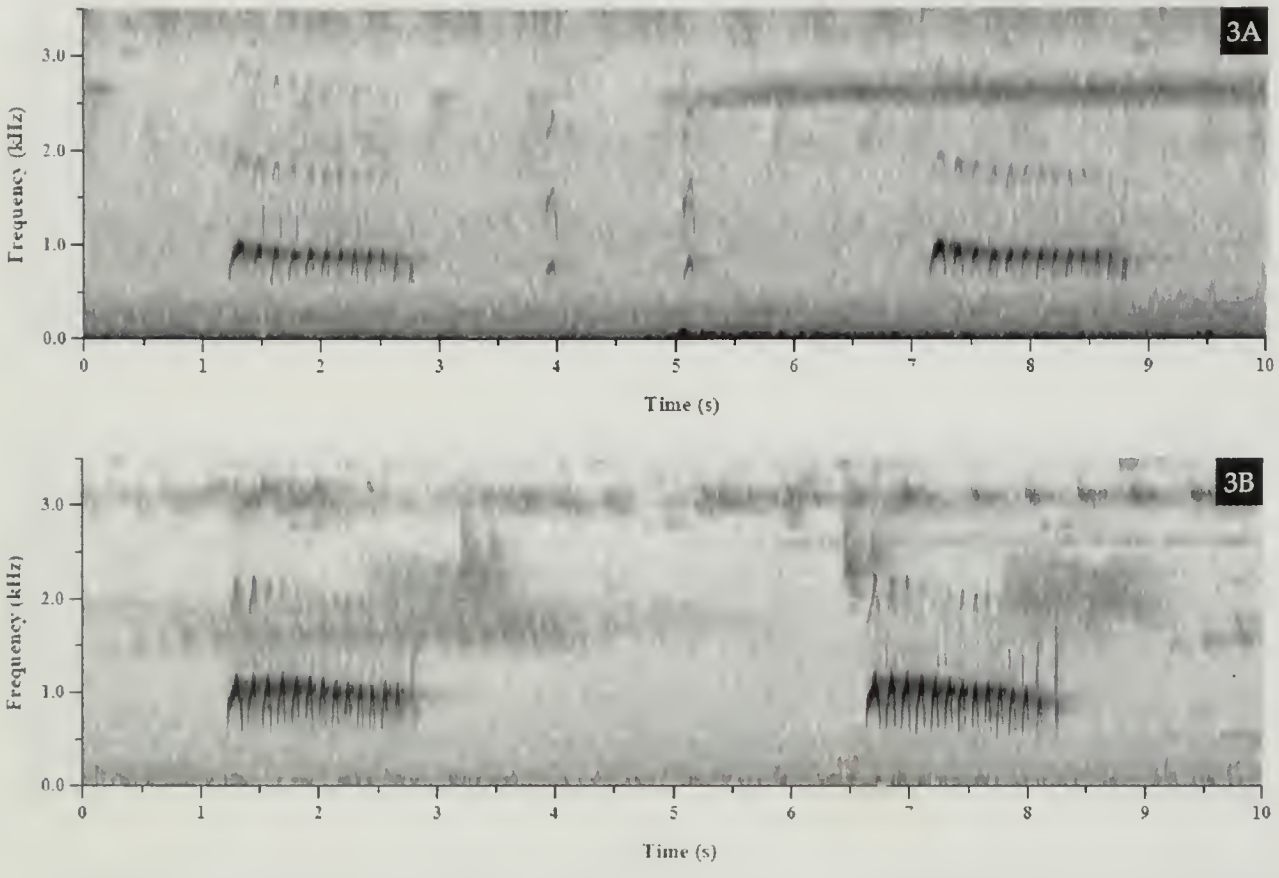

Figure 3A. Two songs and two calls by Rufous Potoo *Nyctibius bracteatus* recorded following playback of the selection on Naka *et al.* (2008). The song represents a slightly descending series of 12–13 'toots' in 1.5–1.7 seconds. The first note is slightly longer in duration and has a frequency range of 600–1,100 Hz, the last is the shortest in duration and lowest in frequency, with a range of 550–925 Hz. The call represents a soft *uurt* note that is easily overlooked (examples here at 4 seconds and 5 seconds). From recording made on 12 April 2006 at Imataca Forest Reserve, Bolívar, Venezuela (CAM field recording file 2006-BOL295; duration between songs has been reduced).

Figure 3B. Two songs by Rufous Potoo *Nyctibius bracteatus* recorded by M. Cohn-Haft at Parque Nacional Jaú, Amazonas, Brazil (taken from Naka *et al.* 2008, but the duration between songs has been reduced), are almost identical to those recorded by CAM at Imataca Forest Reserve, Venezuela (see above).

was still quite tall, with the larger trees probably reaching 25–30 m. There also appeared to be a sandy component to the soils at this site that was not apparent at the first site.

Rufous Potoo *Nyctibius bracteatus*

On 21 July 2005, DA heard *N. bracteatus* singing from inside the forest along the río Cuyuní *c.*5 km downstream of the bridge (Road 10) over the river west of Las Claritas in southern Bolívar. The song was a well-separated series of descending 'toots'. One individual was subsequently observed for a few seconds as it perched 4 m above the ground and 400 m inside the forest. Although the sighting was brief, this individual was obviously richer in coloration and *c.*30% smaller than a Common Potoo *N. griseus*. It also had an unusual shape, with the head and breast apparently more robust than the lower back, rump and tail. The head, back and wings seemed dark rufous with a few white spots apparent at the sides of the back, and the tail appeared paler and faintly barred. Although one of the earliest records of *N. bracteatus* involved a specimen taken at Cumaka (Snyder 1966), in northernmost Guyana, and apparently no more than 5 km from the Venezuelan border based on the coordinates provided by Stephens & Traylor (1985), DA's sighting is the first

record of the species in Venezuela. Based on a lunar calendar, the moon would have been full on this date; however, DA noted that the skies were overcast during his observation.

In the evening of 12 April 2006, CAM & BED located a single *N. bracteatus* in the Imataca Forest Reserve along an old logging road 6.9 km beyond the bridge over the río Grande (08°06′23″N, 61°38′13″W; *c.*285 m). Like our encounters with *N. leucopterus*, we heard this bird only after playback of the song using a pre-release copy of Naka *et al.* (2008). The calls given were a soft *uurt* that was easily overlooked, but the song was a relatively rapid and slightly descending series of 12–15 owl-like 'toots' that could be described as *whooo, tooo, tooo, tooo, tooo, tooo, tooo, tooo, tooo, tooo, tooo, toot*. CAM recorded numerous calls and four songs by the bird on this evening (Fig. 3A), but without seeing it. CAM & BED returned the following afternoon and, using playback and persistence after dark, they eventually obtained good views of the bird in the midstorey of scrubby forest along a small, dry streambed. The bird wobbled back-and-forth on the branch on which it perched. The description below is based on audio notes recorded by CAM on 13 April 2006. Although the description was made over an extended period of time while studying the bird through a telescope, it nevertheless represents a field description taken while the bird was lit by spotlight, and as such subtle colour differences may exist compared to the appearance of the same bird seen in sunlight (*cf.* Cohn-Haft *et al.* 2007: Fig. 12).

Although this was a relatively small potoo, it was difficult to determine its precise size in the field. Whereas CAM estimated it to be the size of an American Kestrel *Falco sparverius* or perhaps slightly smaller, BED thought it closer in size to a Glossy-black Thrush *Turdus serranus*. Like other potoos, the bird had a characteristic upright posture, and an elongate body, with a relatively short bill, a sloping forehead and a flat-crowned appearance on a proportionately large head. The bill was quite short and broad, yet CAM estimated that it extended beyond the forehead, a distance roughly comparable to that between its base and the rear edge of the eye. The gape flanges extended back to a point just below the eye and the bristles at the base of the bill were long and conspicuous. The bird was also relatively long-winged, with the wingtips reaching about three-quarters of the way to the tip of the tail, which itself was about as long as the rest of the bird including the head. The primary projection appeared to exceed the entire length of the exposed secondaries and the tips of four primaries were visible beyond the tips of the longest secondaries in the closed wing. Seen from below, the undertail-coverts appeared to reach between one-fourth and one-third of the way to the tail tip. Also evident from below was that the tail was strongly graduated, with the outer feathers only about three-quarters the length of the inner rectrices, with the tips of four pairs visible in a stepped pattern on the underside of the tail.

The bird was bright rufous throughout, but there was a weak contrast between a deeper shade that approached rufous-chestnut on the breast and belly, and a paler or more cinnamon-rufous colour on the throat, undertail-coverts and undertail. On the upper belly, just below its junction with the breast, was a row of white semi-circles, each of which had a narrow black line above and a more jagged black line below (with this latter margin also sometimes indented along its lower border). A complementary set of white spots formed a U-shaped ring that was conspicuous along the outer edge of the undertail-coverts, which otherwise were faintly barred on a background of bright cinnamon-rufous. The outer rectrices, as seen on the undertail, had six black bands contrasting with the rufous background. The other rectrices were also barred, with the bars on the outer webs of these feathers slightly bolder than those on the inner webs.

The upperparts, wings and uppertail were reddish brown and thus marginally less rufous than the underparts. The wing-coverts were dark rufous-chestnut with a mottled or finely barred appearance, but without a bold pattern. We never noted the series of white

spots that should have been apparent on the scapulars. The remiges were also a dark reddish brown to rufous-chestnut. The secondaries appeared to have dark centres, a diffuse rufous fringe on the outer web and a mostly rufous inner web. The primaries visible in the closed wing were generally browner (less reddish) than the tail, but with a reddish-brown fringe along the outer web that was moderately conspicuous. The exposed primary tips were dark brown with a paler fringe. The uppertail was again relatively rufescent with indistinct, dark barring.

The eyes appeared to be conspicuously white with contrasting black pupils. What was visible of the lower mandible appeared to be pale, but the feathering on the chin extended nearly to the tip of the bill. We failed to note the coloration of the upper mandible, legs and feet.

More recently, during a rapid assessment of the upper río Cuyuní (Lentino *et al.* 2009), on 19 January 2008 at *c.*04.30 h, DA heard a single *N. bracteatus* singing *c.*50 m from a camp along the río Uey, a tributary of the Cuyuní, in southern Bolívar (06°04′15″N, 61°28′44″W; 150–180 m). The song was a single sharp 'toot' followed by a descending series of well-separated 'toots' that ended abruptly. This song was readily differentiated from that of Amazonian Pygmy Owl *Glaucidium hardyi*, which gives a faster and softer series of notes that fades at the end. DA searched this area over the next 12 days but heard no response to playback and he never saw the bird; however, the morning on which DA heard this bird was one of few that he was at this site when it was not raining at dawn.

Unpublished records of both species in Brazil

During field work in Brazil, CAM documented records of *N. leucopterus* at two sites in southern Amazonia not plotted by Claessens *et al.* (2005). *N. leucopterus* was encountered on multiple occasions in the Floresta Nacional do Tapajós, Pará, where it appeared to be fairly common. Singles were heard in 1999, both along the entrance road to the Base de Sucupira (near km 117 on the Santarém–Cuiabá road (BR-163); 03°21′21″S, 54°56′58″W) on 24 August, on 19–20 September, and again on 5 October, and also along a logging road at km 83 on the BR-163 on 25 and 29 August (with two heard and one seen on the first date). At the first of these sites, a narrow road traversed tall *terra firme* forest, but the forest along the logging road at km 83 was scrubbier and the canopy was more uneven as a result of selective logging (see Henriques *et al.* 2003 for a more detailed description). At another southern Amazonian site, CAM repeatedly heard and recorded the vocalisations of up to three *N. leucopterus* on 7–14 December 2000 at Fazenda Toshiba, 8 km east-northeast of Careiro do Castanho in Amazonas (03°47′41″S, 60°17′48″W). The birds at this site were along a narrow road through *terra firme* forest with a canopy of 25–30 m and a few taller emergents. One bird was within 200 m of the forest edge but the others were further into the forest. This site, *c.*100 km south of Manaus, is in a region of predominately white-water rivers, and thus unlike most sites where we and others have found the species. Audio recordings from both sites (e.g., Fig. 1E), as well as one from the Floresta Nacional do Caxiuanã (Fig. 1F), were included in the compilation by Marantz & Zimmer (2006), and the records from the Floresta Nacional do Tapajós were mentioned in Henriques *et al.* (2003). Taken together, these records represent a significant range extension for the species along the south bank of the Amazon across much of the south-east part of the basin. As a whole, our recent records of the species from southern Amazonia come from a variety of sites and a suite of habitats, all in *terra firme* forest and sometimes far from water. None of these encounters were at sites with a sandy component to the soil, but at least some of the birds at the Floresta Nacional do Tapajós, and those at Fazenda Toshiba, were along roads through disturbed or selectively logged forest.

Predating the Venezuelan records of *N. bracteatus*, CAM & M. Cohn-Haft heard the species under a nearly full moon on 31 December 1998 near the indigenous community of Iá-Mirim (00°15′45″N, 66°38′25″W), at km 85 on the BR-307, the road from São Gabriel da Cachoeira to Cucuí. Cohn-Haft was able to record the songs of this bird, but despite extensive searching we were unable to obtain a visual confirmation because the bird was singing from the mid levels of an especially dense part of the forest. Although we did not examine closely the habitat where we heard the bird, the region in general is one in which low-stature *terra firme* forest forms a matrix with swampy woodlands and savannas on sandy soils (locally termed *campinarana* or Amazonian *caatinga*), and thus a close match to the habitat for the species described by Alvarez & Whitney (2003). This site is *c.*60 km south-west of the Venezuelan border and barely more than 100 km from the nearest point in Colombia.

Discussion

We report the northernmost records of *N. leucopterus* and almost the northernmost for *N. bracteatus*, the first records of both species in Venezuela, and previously unpublished records of these species in southern Amazonian Brazil (*N. leucopterus*) and in north-west Brazil (*N. bracteatus*). Although both species remain poorly known, an emerging pattern suggests that these potoos are widespread in Amazonia (as predicted by Cohn-Haft 1999), where they occur from French Guiana west to eastern Peru and across much of Amazonian Brazil (see Claessens *et al.* 2005 for a map of localities for *N. leucopterus*). *N. bracteatus* alone is known from Bolivia, Ecuador, and from at least historical records attributed to Colombia (in the 'Bogotá' collections) (Hilty & Brown 1986, Ridgley & Greenfield 2001; S. K. Herzog pers. comm., T. M. Donegan pers. comm.), and *N. leucopterus* was recorded recently in Surinam, where *N. bracteatus* is unknown (Ottema *et al.* 2010).

Although both species were virtually unknown in life until *c.*20 years ago (e.g., Collar & Andrew 1988), the recent discovery of their vocalisations, their preferred habitats, and that they sing primarily during the short period of the full moon (Cohn-Haft 1993), has resulted in the number and geographic spread of records of both species increasing rapidly. Given their known distribution, we have no doubt that both species will soon be found in Amazonian Colombia, *N. bracteatus* in Surinam and *N. leucopterus* in Ecuador. Moreover, recent reports of *N. leucopterus* in western Brazil in the states of Acre and southernmost Amazonas (Alvarez & Whitney 2003) further suggest that the species occurs in neighbouring Bolivia, where there is already at least one unpublished record of *N. bracteatus* by the late T. A. Parker (S. K. Herzog pers. comm.). The picture that has emerged over the past 20 years supports Cohn-Haft's (1999) contention that both species occur throughout the lowlands of Amazonia.

Cohn-Haft (1993) speculated that *N. leucopterus* is probably common in the canopy of the *terra firme* forests north of Manaus, which is supported by encounters by CAM with the species at the Floresta Nacional do Tapajós, Fazenda Toshiba and Imataca Forest Reserve, all involving multiple birds found opportunistically amid extensive forest. Given that the species appears to be at least relatively numerous where it does occur (see also Ridgely *et al.* 2005), we agree with Claessens *et al.* (2005) that its recent discovery in Amazonia combined with the relative scarcity of encounters since its rediscovery 20 years ago probably reflects the paucity of field work conducted in tropical forests at night and that potoos sing consistently during only a few nights per month at the peak of the full-moon cycle (Cohn-Haft 1993), but it is possible that the species is also somewhat localised. Further complicating the discovery of the Venezuelan birds was that even at the peak of the full

moon during the latter part of the dry season, these birds sang only occasionally and only after playback of recordings or whistled imitations.

Some workers have suggested that *N. leucopterus* occurs primarily in forests with either a sandy component to the soil, deeply weathered clays in black-water regions, or other nutrient-poor soils (Alvarez & Whitney 2003, Whitney *et al.* 2003), and that it prefers primary forest (Peres & Whittaker 1991, Cohn-Haft 1993, 1999, Ridgely *et al.* 2005). However, our observations in somewhat disturbed forest support encounters by other workers who have found this species at forest edge or in fragments, which together suggest that *N. leucopterus* can tolerate some disturbance. We have also found this species in a variety of forest types in both black- and white-water regions, and on a variety of soil types, so it may be less of a specialist than sometimes thought, provided that an intact forest structure and tall trees remain.

Contrasting our experience with *N. leucopterus*, which appears to be relatively numerous where it does occur, *N. bracteatus* appears either local, more restricted in its habitat preferences, rarer overall and more sparsely distributed across its broad Amazonian range, or not particularly vocal. Despite moderate familiarity with its vocalisations, CAM has heard *N. bracteatus* only twice during extensive field work across much of Amazonia, and he has seen it only once (compared with over a dozen encounters of *N. leucopterus* at four widely separated sites). This species has likewise been considered rare to uncommon even in the regions where it has been recorded (Parker *et al.* 1982, 1994, Ridgely & Greenfield 2001, Ridgely *et al.* 2005, Braun *et al.* 2007, Ingels *et al.* 2008). Our observations further support the contention of Alvarez & Whitney (2003) that *N. bracteatus* favours forests with either a sandy component to the soil, deeply weathered clays in black-water regions or other nutrient-poor soils, so its habitat requirements may be more specialised than those of *N. leucopterus*. M. Cohn-Haft (pers. comm.) further clarified that the species occupies principally in understorey and mid levels of *terra firme* forest, but that within this forest type, *N. bracteatus* frequents both continuous tall forest and *caupinarana* vegetation growing on saturated soils with many palms in the understorey. Also, unlike *N. leucopterus*, *N. bracteatus* may occur in well-developed second growth because it does not depend on the truly large trees and tall canopy favoured by *N. leucopterus* (M. Cohn-Haft pers. comm.). As in the case of *N. leucopterus*, however, familiarity with the song and extensive field work on moonlight nights using playback seems to be key to finding the species (see Ingels *et al.* 2008).

Available recordings of the vocalisations of both species are too few to even begin to document geographic variation, but it may be useful to provide a summary of the vocalisations that we have noted (see also Figs. 1–3). We found the song of *N. leucopterus* to be a clear, descending whistle of 4–7 seconds that ranges from 1,750–1,275 Hz, and as such, the descriptions by Cohn-Haft (1993, 1999) are accurate apart from the published duration of 3.5–4.0 seconds being shorter than most of the songs we have recorded in Amazonia. Still, given that the songs in Figs. 1A–B represent the same individual, it would appear both that song duration is more variable individually than geographically and that a terminal note at the end of the song may reflect aggression following playback or a territorial encounter. Similarly, the more steeply descending song in Fig. 1C seems to reflect either individual variation or the motivational state of the bird. The few songs by birds recorded in the Brazilian Atlantic forest that have been examined spectrographically were shorter in duration, slightly lower in frequency, and less obviously descending than those of Amazonian birds (Whitney *et al.* 2003); nevertheless, when heard in the field, these two populations sound remarkably similar (Whitney *et al.* 2003, Costa *et al.* 2010). We would describe the species' call as a soft *wert* or *pwit* note, and thus perhaps less sharp

than suggested by the published descriptions of *bweep* (Cohn-Haft 1999, Costa *et al.* 2010), yet the calls in our Venezuelan recordings (Fig. 2A) closely match those shown for a bird recorded in the Brazilian Atlantic Forest (Costa *et al.* 2010: Fig. 3). Even fewer recordings exist of the song of *N. bracteatus*, but a spectrographic comparison of songs from Venezuela and north-western Brazil (Figs 3A–B) reveals that they are almost identical, and both match closely a published description of the species' song (Cohn-Haft 1999) in being a rapid and slightly descending series of 12–15 sharp 'toots' in the range of 500–1,200 Hz and lasting *c.*1.5–1.75 seconds.

In conclusion, we stress, as did Cohn-Haft (1993), the importance of avifaunal surveys, which will continue to reveal poorly known and, potentially, new species, even at some of the best-known Neotropical sites, such as the Imataca Forest Reserve east of El Palmar, where ornithologists and birdwatchers have made routine visits since the 1970s (e.g., Goodwin 2003).

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The taxonomic status of *Casuarius bennetti papuanus* and *C. b. westermanni*

by Richard M. Perron

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Summary.—Because of confusion in depictions by J. G. Keulemans, Walter Rothschild's monograph on cassowaries wrongly illustrated and described *Casuarius papuanus*. The description and sketch referred in fact to *C. westermanni* and this has led to over a century of incorrect nomenclature in scientific and other publications. A revision is proposed here.

Taxonomy of the cassowaries has long been confused. Forty-eight taxa have been described, of which Peters (1931) recognised 30 that he grouped into six species, two of them he listed as 'range unknown'. In his revision of this work, *c.*50 years later, Mayr (1979: 7) commented that 'Nothing is certain about the classification of the cassowaries except the fact that there are 3 species', namely Double-wattled Cassowary *Casuarius casuarius*, Dwarf Cassowary *C. bennetti* and Single-wattled Cassowary *C. unappendiculatus*. Based on then-current knowledge, he declined to recognise any subspecies, but pointed out available names should subspecific nomenclature be required. Not everyone agreed with Mayr, for instance Wolters (1982) and Howard & Moore (1984) listed several subspecies, but subsequently Folch (1992), Dickinson (2003) and Clements (2008) followed Mayr's approach, and an adequate revision setting out a defensible subspecific taxonomy has still not been produced.

Despite this, it seems important to point out an apparent misapplication of subspecific nomenclature within the species *Casuarius bennetti* Gould, 1857. The nominate form was described from New Britain specimens, and subsequently an array of other subspecies was described from New Guinea. *C. bennetti* is a montane species found in forest to 3,300 m (Coates 1985, Beehler *et al.* 1986) with an estimated range of *c.*258,000 km^2 (BirdLife International 2010) and is known from virtually every mountain range in New Guinea (pers. obs.).

Among New Guinea taxa, birds from the relatively isolated Vogelkop (the Bird's Head Peninsula) in north-west New Guinea have been recognised as being particularly distinctive, notably in the broad white occipital region, such that some authorities (e.g., Davies 2002) accord them species status as *Casuarius papuanus* Schlegel, 1871.

Rothschild (1900: 139) described *Casuarius papuanus* Schlegel, 1871, as 'Adult...Face behind eye, and head white' and illustrated it accordingly (Fig. 1). Subsequently, museum specimens, live zoo examples and in the literature, birds with these features were identified as *C. papuanus*.

Schlegel's (1871) description of the *C. papuanus* holotype, however, makes no mention of a white occipital patch. Likewise, the drawing of this specimen in Rosenberg (1875) also exhibits no white (Fig. 4). In 2007 I photographed the type specimen, 87001, in Naturalis, Leiden, and confirmed that there is indeed no occipital white area (Fig. 5). The first bird to be described with this feature was *Casuarius westermanni* P. L. Sclater, 1874, obtained in Manokwari, Vogelkop, illustrated by Keulemans *in* Sclater (1872) under the erroneous name *kaupi* (as the latter name was found to pertain to a young *C. unappendiculatus*). The

type of *C. westermanni* is now in the Natural History Museum (NHM), Tring, and, although the skin has not aged well (Fig. 2), Keulemans' watercolour compares well with it (Fig. 3).

Rothschild (1931) subsequently recognised his erroneous attribution of these birds with white occipital areas to *papuanus* and suggested they should be designated *westermanni*. Warren (1956) noted both Rothschild's (1931) comments and that the type specimen of *papuanus* had no white patch, but made no further recommendations. Birds with a white occipital patch have therefore continued to be referred to as *papuanus*, although one recent German article (Gedeon & Kleinstäuber 2003) used *westermanni* in referring to a bird in the Vogelkop.

Although *Casuarius* (*bennetti*) *papuanus* remains perfectly valid for Schlegel's type specimen, its use should be restricted to birds matching the description. Quite where Schlegel's holotype should be aligned is still uncertain, but certainly not with birds possessing a predominantly white occipital region. Similarity with *Casuarius claudii*, Ogilvie-Grant, 1911, is the subject of ongoing research.

Many *Casuarius* specimens, both in museums and in zoos, are of uncertain provenance, having been assigned to a given species either on the basis of morphology or sometimes on the locality from where it was assumed to have been acquired. In respect to the 13 birds with a white occipital patch in European museums, the provenance of seven is the Vogelkop (Table 1, Fig. 6). The two from Geelvink Bay may be presumed to also have come from the Vogelkop. The single specimen listed as from the Rawlinson Mountains is perhaps mislabelled because it has been re-designated twice to subspecies which have no physical relationship to it. That presumed to have been obtained on Jobi (Yapen), or alternatively from the Huon Peninsula, may have been traded, but since there was a landbridge between the Vogelkop and Jobi during the last ice age a population there cannot be discounted, despite the lack of verified modern records. Given morphological variability in cassowaries, the custom of native trade in New Guinea, reliable accounts of other Dwarf Cassowary distributions, collections listed in Table 1 and recent sightings in the Arfak Mountains

TABLE 1

Specimens in museums or live birds in zoos of *Casuarius (bennetti) papuanus* or other taxa displaying a white occipital patch, and therefore best assigned to *C. (b.) westermanni* (see text).

Catalogue number		Named	Purported provenance according to label
BMNH 1876.4.24.1	Type	*C. westermanni*	Bird's Head Peninsula, north-west New Guinea
BMNH 1939.12.9.918	Type	*C. goodfellowi*	Jobi Island, Huon Peninsula
BMNH 1939.12.9.914	Type	*C. papuanus rogersi*	Geelvink Bay
BMNH 1939.12.9.901		*C. papuanus edwardsi*	Geelvink Bay
BMNH 1939.12.9.992		*C. edwardsi*	Andai, Bird's Head Peninsula, New Guinea
BMNH 1939.12.9.939		*C. bennetti papuanus*	Unknown
BMNH 1939.12.9.937		*C. bennetti papuanus*	Arfak
BMNH 1916.4.26.1		*C. bennetti hecki*	Rawlinson Mountains, north-east New Guinea
BMNH Gallery 2b		*C. bennetti papuanus*	Unknown
Paris 1877.2017	Type	*C. edwardsi*	North-west New Guinea, Doré
Leiden 103604		*C. papuanus*	North-west New Guinea
Leiden 103605		*C. papuanus*	North-west New Guinea
Leiden 103603		*C. edwardsi*	Arfak, Hattam
Veldhoven1	Live	*C. papuanus*	Unknown
Veldhoven2	Live	*C. papuanus*	Unknown

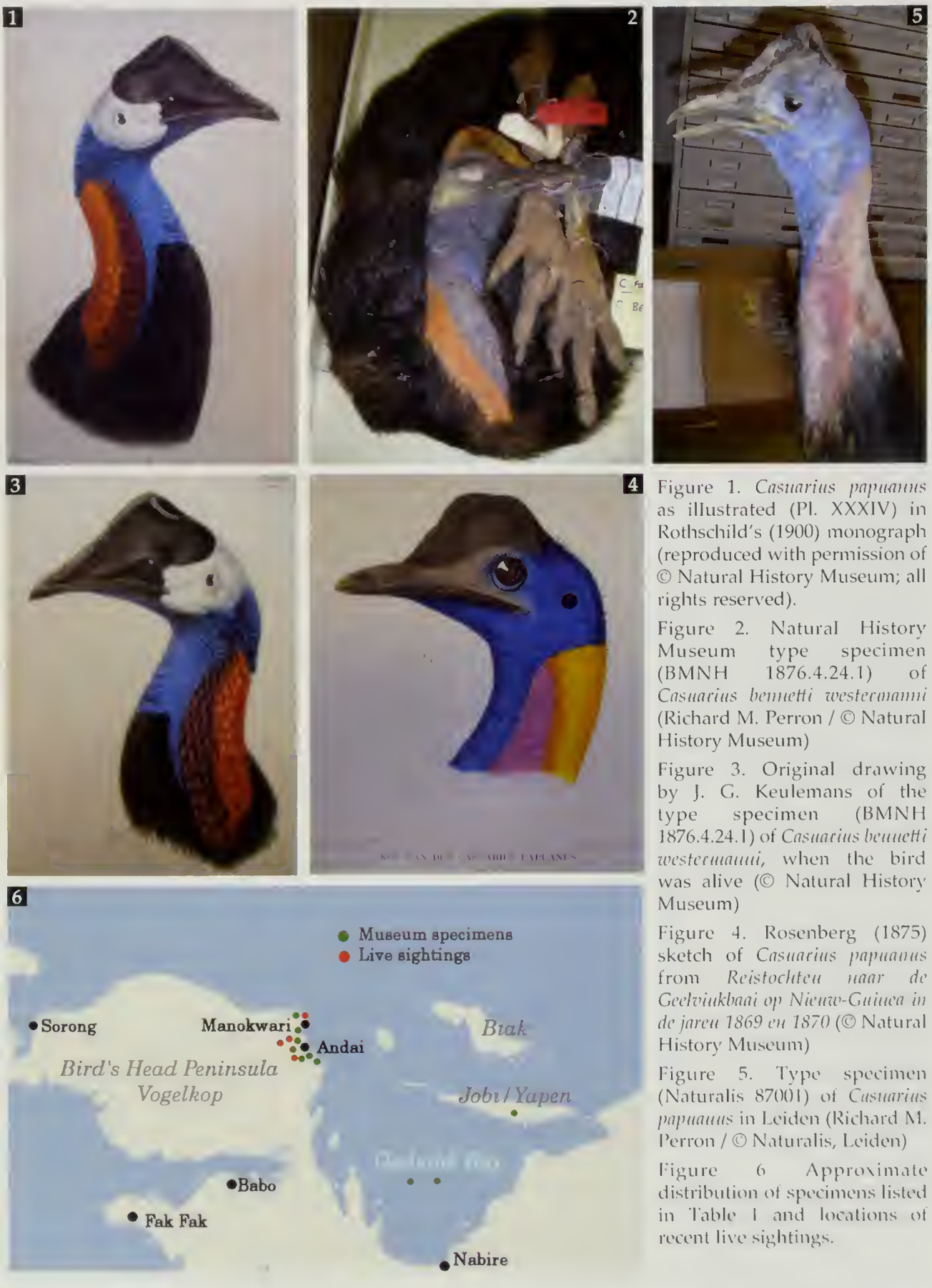

Figure 1. *Casuarius papuanus* as illustrated (Pl. XXXIV) in Rothschild's (1900) monograph (reproduced with permission of © Natural History Museum; all rights reserved).

Figure 2. Natural History Museum type specimen (BMNH 1876.4.24.1) of *Casuarius bennetti westermanni* (Richard M. Perron / © Natural History Museum)

Figure 3. Original drawing by J. G. Keulemans of the type specimen (BMNH 1876.4.24.1) of *Casuarius bennetti westermanni*, when the bird was alive (© Natural History Museum)

Figure 4. Rosenberg (1875) sketch of *Casuarius papuanus* from *Reistochten naar de Geelvinkbaai op Nieuw-Guinea in de jaren 1869 en 1870* (© Natural History Museum)

Figure 5. Type specimen (Naturalis 87001) of *Casuarius papuanus* in Leiden (Richard M. Perron / © Naturalis, Leiden)

Figure 6 Approximate distribution of specimens listed in Table 1 and locations of recent live sightings.

(Gedeon & Kleinstäuber 2003; G. Cubitt *in litt.* 2005, M. Halaouate *in litt.* 2009), it appears certain that the Vogelkop is the provenance of all birds with a white occiput.

The type specimen of *Casuarius papuanus* was obtained by Rosenberg (1875: 84–85) in Andai, a village c.30 km south of Manokwari (a popular destination for foreign travellers),

where he remained for three months in 1870. According to Beccari (1876) and Wichmann (1910), Rosenberg never left the security of Andai during his stay, so he could not have personally caught the bird. The Dutch missionary W. H. Woelders (1877) lived in Andai and is known to have facilitated the acquisition of specimens for visitors, making it probable that the type of *C. papuanus* came via his auspices. Since Papuan and Malayan traders were, and still are, constantly plying the shores of New Guinea, it is not unreasonable to conjecture that the specimen's provenance could have been some distance from Andai and that it was not obtained in the Vogelkop. Indeed, Rosenberg was known for his unreliable information (Salvadori 1882: 210) and it is perfectly possible that he obtained the type somewhere else entirely. In this respect, it is worth mentioning that the type is a female and was sold to Leiden with a chick as a syntype—Rosenberg (and the museum) almost certainly did not know that chicks only accompany males. The type specimen of *C. b. papuanus* is the only known *C. bennetti* specimen without a white patch said to originate in the Vogelkop. The single sighting (B. M. Beehler *in litt.* 2010) in the Arfak Mountains of a bird without a white patch requires clarification, as it is hardly feasible that two forms inhabit the same habitat except via human introduction.

On balance, a re-labelling and descriptive revision of all birds with a white occipital region, previously designated *papuanus, goodfellowi, rogersi or edwardsi*, should be undertaken using the name *Casuarius bennetti westermanni* P. L. Sclater, 1874.

It is too early for any re-evaluation of the number of *Casuarius* species, but morphologically *C. b. westermanni* should be recognised as a valid subspecies under the 75% rule (Amadon 1949). Ongoing personal research reveals that the mtDNA of the two live specimens (ISIS 2009) of *C. b. westermanni* in Table 1 differs significantly from that of both *C. bennetti* (Genbank CBU76037) and *C. b. hecki* (ISIS 2009).

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First record of Purple Swamphen *Porphyrio porphyrio* in the Federated States of Micronesia, with remarks on vagrants and recently established populations of rallids in Micronesia

by Donald W. Buden, John Wichep & Stan Fal'Mngar

Received 6 August 2010

SUMMARY.—We report the first record of Purple Swamphen *Porphyrio porphyrio* in the Federated States of Micronesia (FSM) based on a specimen captured and photographed in Yap in 2004. In coloration and pattern it resembled the *melanotus* subspecies group from the southern part of the species' range, and it probably reached Yap from the Australia / New Guinea region or Palau. However, certain identification as to subspecies and provenance is not possible. Records of other vagrants and recent colonists of rallids in Micronesia are reviewed and include the first sightings of Common Moorhen *Gallinula chloropus* in Chuuk State, FSM.

Purple Swamphen *Porphyrio porphyrio* ranges from Africa and southern Europe east to the Philippines and south to Australia, New Guinea, New Zealand, Palau, and the islands of south-west Oceania (Taylor 1996). It is also introduced in southern Florida, USA (Pranty *et al.* 2000, Johnson & McGarrity 2009). We report the first record of a Purple Swamphen in the Federated States of Micronesia (FSM) from a bird photographed on the main island of Yap in 2004 (Fig. 1). In reply to a query from DWB regarding unusual birds encountered by quarantine inspectors in the FSM, JW recalled seeing a photograph of a large bluish-coloured bird taken on Yap several years earlier, which had never been identified. JW contacted A. Fagolur of FSM Quarantine, Yap Station, who furnished a copy of the photograph and stated (pers. comm.) that the bird was brought to the Yap State FSM Quarantine Office by someone from the village of Yinuf, near Yap High School in July 2004. We later received additional photographs taken by M. Falanruw. SF interviewed those people directly involved in the capture and subsequent handling of the specimen. Brothers, D Gilmoon and S. Guwaathag first saw the bird in a grassy area near their house and caught it when it ran into a taro patch; it was unable or did not attempt to fly. The bird was photographed by staff from the Yap State Division of Agriculture and Forestry and was left in the possession of the brothers. It died *c.*3 days later and was buried. The partially decomposed carcass was later exhumed at the request of M. Falanruw (Yap Institute of Natural Science) and stored in a freezer. The specimen remains in storage at the time of writing pending sampling for DNA and preparation as a skeleton (M. Falanruw & H. D. Pratt pers. comm.). The bird presumably reached the island by natural dispersal, as the species is unknown in captivity in Yap. Although *P. porphyrio* does not regularly migrate long distances, it may move seasonally and locally in response to habitat changes (Taylor 1996). The species is highly dispersive (Steadman 2006) and has been recorded moving up to 1,000 km (Grussu 1999).

We sent the Division of Agriculture photograph of the swamphen on Yap to personnel of the American Museum of Natural History, New York (AMNH), Auckland Museum (AIM), Australian Museum, Sydney (AMS), Museum für Naturkunde, Berlin (ZMB), Museum of Comparative Zoology, Cambridge, MA (MCZ), Natural History Museum, Tring (NHM), and National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), for comparison with various subspecies of *P. porphyrio*. We also

compared it with descriptions in Taylor & van Perlo (1998), and with photographs of living *P. p. pelewensis* taken in Palau. Species and subspecies limits within the *P. porphyrio* complex are variously interpreted by different authors, as reviewed by Sangster (1998). We follow Taylor (1996) and Taylor & van Perlo (1998) in recognising 13 subspecies within six subspecies groups. Five of the six groups occur in the north and west of the species' range (Africa and Eurasia, to the Philippines); the Yap bird does not match well in coloration and pattern with any of those groups and most of these subspecies are unlikely on

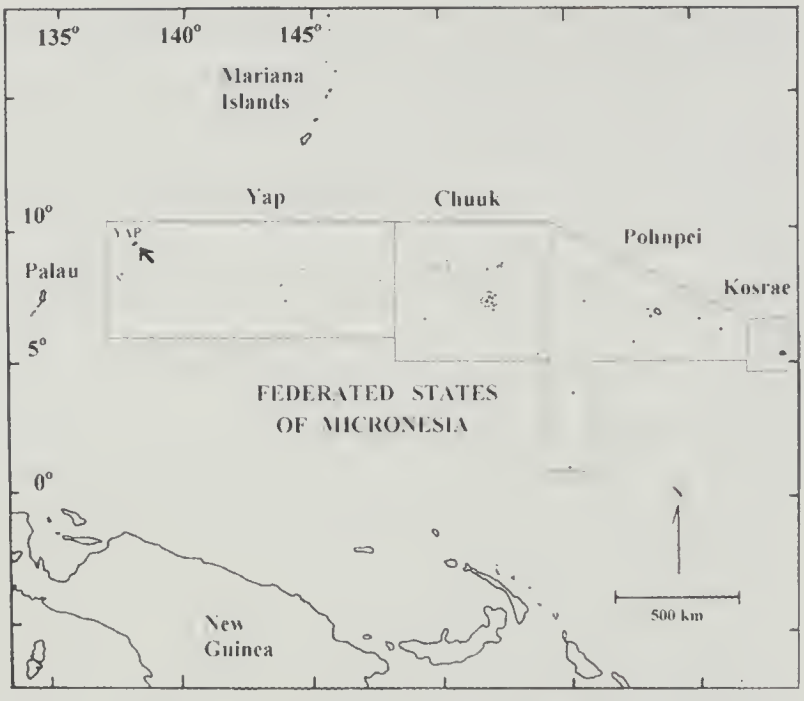

Figure 1. Location of Yap and the Federated States of Micronesia in the tropical western Pacific Ocean.

Figure 2. Purple Swamphen *Porphyrio porphyrio* captured in Yap, Federated States of Micronesia, July 2004 (M. Falanruw)

geographic grounds. That closest to Yap geographically, *P. p. pulverulentus*, which is endemic to the Philippines, is much paler and dusty bluish grey. The south-east of the species' range is occupied by five subspecies that comprise the *melanotus* group. In coloration and pattern the bird from Yap appears to resemble many examples of *P. p. melanotus* from Australasia. It also resembles some photographs of *P. p. pelewensis* from Palau, *c.*400 km to the south-west, and geographically the population closest to Yap (Fig. 2). But specimens of birds from Palau appear darker, with nearly uniform ventral regions, and tend to lack the distinctly pale blue breast evident in the bird from Yap (P. Capainolo & S. Frahnert pers. comm., DWB pers. obs.). In sending the photograph to several curators for examination, we found that the bird also matched some examples of *P. p. samoensis* and *P. p. melanopterus*, at least among the available material (W. Boles, M. LeCroy & P. Capainolo pers. comm.). We are confident that the bird from Yap is an example of the *melanotus* group, possibly from Palau or the Australia-New Guinea region, based on geographic proximity and overall appearance, but in view of the variability within subspecies in the *melanotus* group (Taylor & van Perlo 1998) and the broad overlap in specimens (W. Boles pers. comm.), certain identification of the Yap specimen as to subspecies and assessment of its origin based on the available photograph is not possible. There is no indication that the swamphen photographed on Yap was anything other than an accidental visitor or stray; it remains the only record.

Rallids in Micronesia: vagrants and recent colonists

Rallidae have a cosmopolitan distribution, being absent only from polar regions. A tendency to wander and excellent over-water dispersal has resulted in their successfully colonising some of the most remote oceanic islands (Olson 1973, 1999). Many of the early colonists rapidly evolved into flightless insular endemics, most of which have since been extirpated through human exploitation, habitat modification and introduction of predators (Steadman 2006). Some contemporary volant species are renowned for remarkable incidents of long-distance vagrancy (Livezey 1998), with many examples given by Remsen & Parker (1990).

In the most recent checklist of the birds of Micronesia, Wiles (2005) recorded 11 living or recently extinct species of rallids, four of them vagrants to one or more islands, and including birds that may have dispersed from islands within the region as well as those from outside it: Red-legged Crake *Rallina fasciata* and Rufous-tailed Bush-hen *Amaurornis moluccanus* in Palau, White-browed Crake *Poliolimnas cinereus* in the Marshall Islands, and Eurasian Coot *Fulica atrata* on Guam and in the Commonwealth of the Northern Mariana Islands (CNMI). The dates for these vagrants range from as early as 1896 for one of the two records of *F. atrata* on Guam (Baker 1951) to 2003 for the other (Wiles *et al.* 2005). Pratt *et al.* (2010) recently added the first record of *F. atrata* in the FSM based on a bird on the main island of Yap in February 2003. A particularly noteworthy example of apparent long-distance vagrancy involving a rallid in Micronesia is a Watercock *Gallicrex cinerea* photographed on Kosrae, FSM, in May 2010, *c.*4,000 km from the nearest breeding population in the Philippines and at least 3,000 km from the nearest known migrants or extralimital records in southern Japan (Buden & McKinlay 2010).

Two rallids have recently established breeding populations in Micronesia, probably within the past 30–40 years. Common Moorhen *Gallinula chloropus* probably became established on the main island of Yap during the mid to late 1980s (Wiles *et al.* 2000, 2004), and on Rota, CNMI, during the early to mid 1990s when artificial ponds at a recently constructed golf resort provided the only suitable habitat (Worthington 1998). Moorhens had been unrecorded on Rota in historical times but bones from archaeological digs indicate they occurred prehistorically, apparently when natural wetlands were presumably present

(Stinson *et al.* 1991, Steadman 1992). The recently established population on Rota probably originated from within the Marianas, whereas that on Yap could have originated from any one of several sources, including the Marianas, Palau or South-East Asia. Four *G. chloropus* observed in a marsh adjacent to the commercial district on Weno (= Moen) Island, Chuuk, by M. Beaman on 19 December 2005 (D. A. Scott pers. comm.), two observed by D. A. Scott *et al.* on 8 December 2008, three on 16 January 2010 (Hornbuckle 2010; J. Hornbuckle pers. comm.), a pair photographed by G. McKinlay (pers. comm.) on 14 May 2010, and five, including two juveniles, seen by D. A. Scott *et al.* (pers. comm.) on 6 December 2010, all at the same marsh on Weno, are the first confirmed records in Chuuk State, FSM. However, several Chuuk islanders shown photographs of this species during interviews by DWB in July 2010 claimed to have seen it on Weno and on other islands in Chuuk Lagoon, including Tol and Parem, and as long ago as 20–30 years previously, when, they said, the birds were more numerous. An approximately equal number of people queried were unfamiliar with the species. The status of *G. chloropus* in Chuuk merits further investigation; the records may pertain to residents or migrants, or both.

In another example of colonisation of Micronesia in recent decades, Buden & Retogral (2010) reported the range expansion of White-breasted Waterhen *Amaurornis phoenicurus* into the region based on the recent (2009) discovery of a breeding population on Woleai Atoll (and reports by islanders of breeding or presumed breeding on three adjacent atolls) in the Outer Islands of Yap, as well as the first record in Palau, based on a bird photographed by M. Vereen during late October–early November 2009. Woleai islanders first noticed the birds on their atoll around the 1970s, apparently near the start of a period of range expansion in the species that has continued to the present (Buden & Retogral 2010). The islanders reported that the birds are usually encountered in taro patches, which are wet swampy areas where one or more species of aroid are cultivated as subsistence crops.

The rallids recorded as vagrants or as recent colonists in Micronesia are species that are migratory or dispersive in at least part of their ranges, and all inhabit marshes or other wetlands. Suitability of such habitats for rallids may change seasonally or be impacted irregularly by droughts, floods and degradation by human activities. Remsen & Parker (1990) remarked that even rails and gallinules thought to be sedentary can appear at unpredictable times and places dictated by changes in their habitat. Although many rallids are capable of sustained flight, they tend to be weak flyers that are likely to be driven off-course by strong winds, presumably accounting for the many examples of vagrants or accidental visitors.

To what extent changes in habitat and movements of birds in different parts of their range account for the increased incidence of rallids in Micronesia is uncertain. However, the increase in knowledgeable observers visiting the islands may be a major contributing factor. Records of Watercock on Kosrae, the two separate sightings of moorhens in Chuuk, White-breasted Waterhen in Palau, and European Coot in Yap were contributed in part by avocational birders. Given the still somewhat sporadic observations on many islands throughout Micronesia, some of them seldom if at all visited, the actual number of vagrants among rallids and other birds is probably much higher than reported.

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First record of Réunion Black Petrel *Pseudobulweria aterrima* on Mauritius

by R. V. Tatayah, C. G. Jones, D. Birch & M. Salamolard

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Réunion Black Petrel *Pseudobulweria aterrima* breeds on the island of Réunion in the south-west Indian Ocean, where its population is estimated at 45–400 pairs (average 250 breeding pairs), or a maximum of 1,000 birds at sea (Attié *et al.* 1997, Cheke & Hume 2008), making it one of the rarest seabirds in the world (Le Corre *et al.* 2003). Recent estimates indicate that the breeding population may be much lower than estimated, probably just a few dozen pairs (Riethmuller *et al.* in prep.). It is treated as Critically Endangered (BirdLife International 2009). A subfossil mandible was collected in cave deposits on Rodrigues, where the species perhaps nested in the past (Bourne 1968). *P. aterrima* is increasingly known as Mascarene Black Petrel (Attié *et al.* 1997, Le Corre *et al.* 2003), a name supported by its recorded presence on all three of the Mascarenes.

Although first collected and drawn for Commerson around 1770 (Cheke 2009), *P. aterrima* was not described until 1856 and ten had been collected by the end of the 19th century, of which only four survive (Jouanin 1970). No further sightings were made until 1970 (Hirschfeld 2008), by when the species was considered probably extinct and a reward had been offered for its rediscovery, which led to the capture of two grounded birds on Réunion in 1970 and 1973 (Jouanin 1987). A freshly dead bird was found in 1995 (Attié *et al.* 1997). To date, no nests have ever been found. However, calls of Réunion Black Petrel have been heard during the breeding season (the austral summer) on cliffs at 1,000 m (Riethmuller *et al.* 2003, Hirschfeld 2008) and fledglings have been caught in March.

Since 1995, a rehabilitation programme on Réunion cares for birds found stranded under coastal streetlights (Le Corre *et al.* 2002, 2003). Due to the Réunion-wide awareness and rescue campaign, seabirds are saved from probable death due to poaching, dehydration, starvation, predation by cats and dogs, and car strikes; the survivors are ringed prior to release. By 2008, 22 *P. aterrima* (including eight fledglings) had been rescued and 19 were subsequently released (Hirschfield 2008).

On 30 September 2002, DB discovered a roadkill Réunion Black Petrel on the Plaine Champagne Road (Black River Gorges National Park), above the village of Chamarel under the only streetlight in the area (20°43′S, 57°42′E; 647 m). This is the first record of the species on Mauritius. The bird was in almost perfect condition and was sent to the Natural History Museum (Tring), where it was prepared as a study skin (BMNH 2004.5.1; Figs 1–3). It was an adult but the sex could not be determined (K. van Grouw *in litt.* 2004). Morphometrics are presented in Table 1.

TABLE 1
Morphometric measurements of Réunion Black Petrel *Pseudobulweria aterrima* specimen from Mauritius (BMNH 2004.5.1).

Morphometric	Length† mm
Wing (left/right)	255/256
Tail	110
Tarsus	41.6
Bill* (to feathers)	28.5
Middle toe	50.2

† mean of measurements taken by Anthony Cheke and Joanne Cooper.
* bill depth not measured as jaw broken

Workers at a nearby hunting lodge are unfamiliar with the petrel. It is possible that Réunion Black Petrel nests in montane parts of the Black River Gorges, but this is unproven. The habitat is fairly similar to that of the suspected breeding areas on Réunion and non-breeding petrels are known

Figure 1 (left). Dorsal view of Réunion Black Petrel *Pseudobulweria aterrima* specimen (BMNH 2004.5.1) with spread wing (© Natural History Museum, Tring)

Figure 2 (below left). Ventral view of Réunion Black Petrel *Pseudobulweria aterrima* specimen (BMNH 2004.5.1) and spread wing (© Natural History Museum, Tring)

Figure 3 (above). Details of head of the Réunion Black Petrel *Pseudobulweria aterrima* (© Natural History Museum, Tring)

Figure 4 (below). Drawings of the intestines of the Reunion Black Petrel *Pseudobulweria aterrima*, displaced to left and right, showing the lack of intestinal coiling, typical of *Pseudobulweria* spp. (Katrina van Grouw, © Natural History Museum, Tring)

to prospect other breeding sites, despite their philopatric behaviour. *P. aterrima* presumably returns to its nest sites nocturnally to reduce chances of predation. However, shearwaters have become extinct on Mauritius due to the presence of Indian Lesser Mongooses *Herpestes javanicus*, and it is probable that petrels must have become very rare. Alternatively, the bird could have been a vagrant, as in Barau's Petrel *Pterodroma baraui* for instance.

In 1888 Edward Newton, former Colonial Secretary in Mauritius and brother of Alfred Newton, then curator of the Cambridge Zoology Museum made a request to Auguste Lantz, curator of the Muséum de Saint-Denis, Réunion, to obtain Réunion Black Petrels for his collection. Auguste de Villèle, thought to have been the only person to know their nest sites, collected eight individuals in 1889–90 (Jouanin 1970). Six were retained by the museum in Saint-Denis (accession records noted by Jouanin 1970). Unfortunately these specimens have been lost, but two specimens from the series survive (Jouanin 1970, Attié *et al.* 1997), in the Museum National d'Histoire Naturelle, Paris, and the University Museum of Zoology, Cambridge, UK.

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First description of the nest of Undulated Antpitta *Grallaria squamigera*, from south-west Ecuador

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The 31 species of *Grallaria* antpittas (Grallariidae) are principally of Andean distribution and are among the most secretive of Neotropical passerines (Krabbe & Schulenberg 2003). Of the 15 species that occur in Ecuador, the nests of ten have been described only during the past seven years (e.g., Freile & Renjifo 2003, Price 2003, Martin & Dobbs 2004, Greeney & Martin 2005, Greeney *et al.* 2006, Martin & Greeney 2006, Greeney *et al.* 2009, Juiña *et al.* 2009, Solano-Ugalde *et al.* 2009, Greeney & Juiña 2010). These studies have left only three species in Ecuador with undescribed nests and have made Ecuador's antpitta fauna one of the most thoroughly studied (Greeney *et al.* 2008, Freile *et al.* 2010). Of the unstudied Ecuadorian *Grallaria*, Bicoloured Antpitta's *G. rufocinerea* range extends south from Colombia only to the extreme north-east and Ochre-striped Antpitta *G. dignissima* is the only lowland Amazonian member of the genus. The final species, Undulated Antpitta *G. squamigera*, is a fairly widespread inhabitant of humid montane forests (at 2,200–3,800 m) from western Venezuela to western Bolivia (Ridgely & Greenfield 2001, Krabbe & Schulenberg 2003, Freile *et al.* 2010). Here we describe the nest, egg and hatchling of Undulated Antpitta from south-west Ecuador.

Methods and Results

We found a nest of Undulated Antpitta on 25 February 2010 at Cerro Huachaurco (04°03′74″S, 79°87′36″W), at 3,020 m, near Huachanama, prov. Loja. On discovery, at 17.00 h, an adult was present and allowed us to approach to within 30 cm before departing the nest. The nest contained an addled egg and a nestling that was no more than one day old. We returned the following day at 11.15 h to measure the nest, egg and nestling. The egg was turquoise with brown and pale lavender spotting, heaviest at both ends but more so at the larger end. It measured 33.5 × 28.0 mm. The nestling's skin was dark pink to greyish, with dark legs and feet. The bill was dusky with an orange mouth lining and slightly brighter rictal flanges. The coloration of both the lining and flanges was not as bright as in other *Grallaria* spp. we have observed. The nestling was mostly covered by dense tufts of black natal down and weighed 16.5 g. We returned on 1 March at 07.15 h, at which time an adult was brooding, leaving the nest only after we approached to within 1 m. The nestling weighed 36 g and was similar in coloration to previously. Pin feathers had broken through the skin on all contour feather tracts and primary pin feathers were *c.*5 mm long and unbroken. We were unable to monitor the nest further.

The nest was a bulky, cup-shaped structure composed mostly of green moss intermixed with a few sticks and dead leaves. It was lined with dark, flexible fibres and rootlets, as well as a fair number of needles from the stand of introduced pines just 30 m away. The nest was 2.5 m above ground and supported by the crossing of several nearly horizontal branches, most less than 5 cm in diameter (but two were *c.*10 cm diameter). From below it appeared to be little more than a large clump of naturally collected debris, and was likely built onto a pre-existing collection of material. Externally, the nest was slightly oblong and measured 27 × 25 cm wide and 22 cm tall. The internal cup measured 13 × 14 cm wide by *c.*6–7 cm deep.

The forest surrounding the nest was scrubby second growth, with a fragmented canopy *c.*10–15 m in height.

Discussion

In general form and appearance the nest, egg and nestling of Undulated Antpitta are similar to those of other *Grallaria* (Greeney *et al.* 2008). Unlike most, however, the turquoise egg is rather heavily spotted. As sample sizes are still small for most species, and better-studied species show variation in this respect (Greeney & Martin 2005), the significance of heavily marked eggs in this species is unclear. Undulated Antpitta joins a number of other species of *Grallaria* in building its nest supported by multiple small branches rather than in well-supported situations such as tree trunks (Greeney *et al.* 2008). It shares this trait with Plain-backed Antpitta *G. haplonota* (Greeney *et al.* 2006), Chestnut-crowned *G. ruficapilla* (Martin & Greeney 2006), Watkins's *G. watkinsi* (Martin & Dobbs 2004), Chestnut-naped *G. nuchalis* (Juiña *et al.* 2009), Stripe-headed *G. andicola* (J. Fjeldså *in* Greeney *et al.* 2008) and Tawny Antpittas *G. quitensis* (Greeney & Martin 2005). Of all of these, however, it shares the predominance of moss in the nest with only Stripe-headed and Tawny Antpittas. Observations on several nests in north-west Ecuador, presumed to be of this species, suggest that the position and composition of this nest is probably typical for Undulated Antpitta (HFG unpubl.).

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New record of Cinnamon Teal *Anas cyanoptera* in Ecuador

by Carlos Camacho & Robert E. Wilson

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Cinnamon Teal *Anas cyanoptera* is widespread throughout much of the Western Hemisphere, with five subspecies (*A. c. borreroi*, *A. c. cyanoptera*, *A. c. orinomus*, *A. c. septentrionalium* and *A. c. tropica*) currently recognised (Snyder & Lumsden 1951, Wilson *et al.* 2010). *A. c. septentrionalium* breeds in western North America and is a common winter visitor to the southern USA and Central America, with small numbers reaching northern South America. South American populations are mainly sedentary or exhibit only small-scale dispersal (Phillips 1923). *A. c. borreroi* is endemic to the east Colombian Andes, whereas the adjacent lowlands are occupied by *A. c. tropica*. Further, *A. c. orinomus* occurs in the highlands of Argentina, Bolivia, Chile and Peru. The most widespread South American subspecies, *A. c. cyanoptera*, occurs throughout the lowlands of Peru to Chile, Uruguay and Argentina, and occasionally wanders to the central high Andes, where it may be found with *A. c. orinomus* (Evarts 2005).

Figure 1. Map of Ecuador showing the locations of Cinnamon Teal *Anas cyanoptera* reports mentioned in the text.

Cinnamon Teal has historically been scarce in the Ecuadorian high Andes and inter-Andean valley, with records of both *A. c. borreroi* and *A. c. septentrionalium* in northern Ecuador. The last record was of a pair of *A. c. septentrionalium* on Laguna de San Pablo, prov. Imbabura, 50 km north of Quito, in 1938 (Ridgely & Greenfield 2001); it was subsequently considered extirpated in Ecuador (Granizo *et al.* 2002). The cause of its disappearance is uncertain (Ridgely & Greenfield 2006) but wetland disturbance seems most likely (MAE *et al.* 2000).

There have been very few recent observations of Cinnamon Teal in Ecuador (Fig. 1). There are two reports, of a male and a pair, at Punta Moreno, Isabela Island, Galápagos, in October and November 2004 (Kostecke & Kostecke 2006), the first records for the archipelago. The species has been reported twice in southern Ecuador: one on Laguna de Llaviuco, Cajas National Park, prov. Azuay (King 1989), for which supporting evidence is lacking, and one at Santa Rosa marshes, prov. El Oro, on 1 June 2003 (R. Ahlman pers. comm.). These reports probably involved vagrant *A. c. cyanoptera* as this subspecies is

widespread in coastal Peru (Schulenberg & Parker 1981, Wilson *et al.* 2010), although in neither case was subspecific identification attempted.

On 11 March 2009, three male Cinnamon Teals were hunted at San Eloy, prov. Manabí (00°54'S, 80°27'W; 330 m) with 40 Blue-winged Teals *Anas discors*. They were shot in a flooded rice field. One of the Blue-winged Teals was banded with a metal ring from Ontario, Canada. Despite the hunters' knowledge of local waterfowl, they were unable to identify the Cinnamon Teals. According to local people, Cinnamon Teal has not been seen in San Eloy for >20 years. All three birds were of similar size and plumage (Fig. 2). The hunters did not allow us to retain any of the birds for further examination. Therefore precise measurements are not available to aid in subspecies identification.

Discussion

General plumage and body size of examined specimens and differences in distribution, abundance and migratory behaviour among subspecies of *A. cyanoptera* suggest that the new record probably involved *A. c. septentrionalium*. The Colombian subspecies (*A. c. borreroi* and *A. c. tropica*) typically possess more spotting than the three specimens examined, and *A. c. borreroi* is dark chestnut-brown (Snyder & Lumsden 1951). In addition, both Colombian subspecies have a restricted range and have been listed as threatened, with <250 individuals remaining for *A. c. borreroi* (Wetlands International 2002). Consequently, the likelihood that the birds belonged to one of the Colombian subspecies is low.

Ridgely & Greenfield (2001) postulated that the high-altitude *A. c. orinomus* could wander from Peru to lowland Ecuador. However, the northern limit of *A. c. orinomus* is dpto. Junín central Peru (Blake 1977, Evarts 2005, Wilson *et al.* 2010) making it unlikely that a vagrant *A. c. orinomus* would wander to central Ecuador. Furthermore, *A. c. orinomus* is the largest subspecies and is easily separated from other subspecies solely on overall body size (Wilson *et al.* 2010). The small size of the San Eloy birds suggests that the most likely candidate subspecies are either *A. c. cyanoptera* or *A. c. septentrionalium*. These two are extremely difficult to differentiate using plumage (Wilson *et al.* 2008); only bill length can be used to distinguish them (Wilson *et al.* 2010). Although Blake (1977) considered that *A. c. cyanoptera* can have spots on the breast, flanks and belly, which are lacking in *A. c. septentrionalium*, of 18 specimens recently collected on the Peruvian coast and held at the University of Alaska Museum (Fairbanks, USA) only 72% have spots on the breast, flanks or rump (REW unpubl.). Therefore plumage is not a reliable character, as the degree and location of spotting is variable.

Figure 2. One of the three male Cinnamon Teals *Anas cyanoptera* shot at San Eloy, prov. Manabí, 5 March 2009 (Carlos Camacho)

The location (San Eloy), which is not part of the typical breeding range of *A. c. cyanoptera*, and the time of year (March) suggest these individuals were

A. c. septentrionalium rather than vagrants from the Peruvian coast. *A. c. septentrionalium* is a fairly frequent migrant to northern South America, albeit in small numbers, and has historically been recorded as far south as northern Ecuador (Ridgely & Greenfield 2006). Furthermore, *A. c. septentrionalium* commonly forms wintering flocks with Blue-winged Teal. That one of the Blue-winged Teals had been banded in Canada suggests the flock came from North America. Although we cannot confirm the subspecies involved, we feel this indirect evidence points to *A. c. septentrionalium*.

This is a significant record, regardless of the subspecies involved, as it is one of only three reports in the last 72 years. Given the threatened status of Cinnamon Teal in Ecuador (Freile & Rodas 2008), this observation increases our current knowledge of its distribution and migration, although long-term monitoring is required to determine if a potential range expansion from the south or if wintering birds from North America are returning to historical wintering sites is the cause. The report also provides further evidence of the importance of documenting plumage characteristics (e.g., presence of spots and overall coloration) and measurements in this species (especially bill length from the posterior edge of the nares to the nail, and wing chord; Wilson *et al.* 2010) to accurately identify birds to subspecies and potentially determine their provenance.

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The Leverian Great Auk *Alca impennis*, its known history

by Justin J. F. J. Jansen

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Fuller (1999) listed all known Great Auk *Alca impennis* mounts and eggs. His book, *The Great Auk*, contains a detailed history of each known specimen and egg, including the Copenhagen museum's 'Winter Auk' (pp. 163–166), which information Fuller based on various sources. However, some of his assumptions were incorrect, and merit correction, namely the date of the Leverian Auction, the year in which the specimen was collected and its history prior to *c.*1842 (Fuller 1999).

The specimen of Great Auk drawn by Edward Donovan in *The natural history of British birds* (1794–1819) in vol. 10, p. 243, was purchased at the Lever Auction. When the specimens from the Leverian Museum were auctioned, in May–June 1806, no fewer than 500 lots were bought by Donovan (Jackson 1985). Amongst them was the Great Auk auctioned on Monday 5 May 1806 as lot 47 for £10.10 (Johnson & Hewett 1979). The annotations made in the reprint of the 1806 catalogue (King & Locheé 1806) were made by Richard Cuming, which copy is now in the Cuming Museum, Southwark, London. The copy consulted in the Natural History Museum, London, contains no annotations. The assumption that the bird was collected in 1815 is therefore impossible. Nor was the Lever Museum auction held in 1818 (Fuller 1999). Edward Donovan's collections were auctioned in 878 separate lots, in 1818, at J. C. Steven's auction rooms, London (Horn & Kahle 1935, Chalmers-Hunt 1976). Thereafter the bird took the (possible) route outlined by Fuller (1999), via Friedrich Wilhelm Benicken, Emil Hage and finally via Johannes Reinhardt into the collection of the Zoologisk Museum at Copenhagen University, Denmark.

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